



Modelling the growth of European beech (*Fagus sylvatica* L.) in Denmark

Nord-Larsen, Thomas

Publication date:
2006

Document version
Publisher's PDF, also known as Version of record

Citation for published version (APA):
Nord-Larsen, T. (2006). *Modelling the growth of European beech (Fagus sylvatica L.) in Denmark*. Center for Skov, Landskab og Planlægning/Københavns Universitet.

Royal Veterinary and Agricultural University
Thesis submitted for the degree

PHILOSOPHIÆ DOCTOR

MODELLING THE GROWTH OF EUROPEAN BEECH
(*Fagus sylvatica* L.) IN DENMARK

THOMAS NORD-LARSEN

January 2006

Royal Veterinary and Agricultural University
Forest & Landscape
Hørsholm
Denmark

Preface

This dissertation is submitted in partial fulfilment of the requirements for the Ph.D. degree at the Royal Veterinary and Agricultural University, Denmark. The project was initiated in October 2002 at the Danish Centre for Forest Landscape and Planning under supervision of Associate Professor Henrik Meilby and Senior Researcher Vivian Kvist Johannsen. The project is part of the programme *Economic Optimisation of Multiple-use Forestry and other Natural Resources* and is funded by the Danish Agricultural and Veterinary Research Council, Danish Centre for Forest, Landscape and Planning and Danish Forest and Nature Agency.

The dissertation was made as an extension of the previous research project *Dynamic Growth Models for Danish Forest Tree Species*. The previous work on developing dynamic models for predicting growth and yield of even-aged oak (*Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.) and Norway spruce (*Picea abies* L.) (Johannsen, 1999) has been a great source of inspiration throughout the making of this dissertation. I therefore gratefully thank Vivian Kvist Johannsen for sharing her experience within this field.

The extensive data that form the basis of this dissertation was made available by numerous forest researchers and technicians through the history of forest measurements in Denmark. The consistency of measurements through several generations of researchers attests to their clever determination to make available the best possible tools for future generations of forest professionals. I would like to take this opportunity to state my admiration for the effort and foresight of these people, who carefully installed more than 200 permanent research plots with European beech and measured and recorded trees, soil and other details without which this dissertation could never have been made. I would also like to state my gratitude to Per Holten-Andersen, who entrusted me with the data and gave me this great opportunity when he left to take on the responsibility as director of the Royal Veterinary and Agricultural University.

During my study I had the great opportunity to work at Oregon State University for six months from January to July 2004. My stay there has served as a great source of inspiration for my work and I am eternally grateful to Professor Dr. David Hann for his help and inspiration during my time in Oregon. I am also indebted to the staff at Oregon State University, Art

and Marylin Berwin, Dawn and Nathan Moyer and Fred Ramsey for their considerate care for me and my family. Finally I would like to thank J.F. Classens Legat and Kristoffer Bramsens Fond for partial funding of the stay at Oregon State University.

During my Ph.D. studies I have met many inspiring, helpful, talented and wonderful people. Your advice, support and encouragement have been invaluable to me. Especially I would like to thank Jens Peter Skovsgaard for sharing his intimate knowledge on almost every permanent sample plot in the history of forest measurements in Denmark. Further I would like to thank Bruce Edward Talbot for commenting on almost every part of this thesis and Peter Stoltze for readily giving his support and advice on typesetting L^AT_EX 2_ε documents.

Thomas Nord-Larsen
Hørsholm, January 2006

Summary

Modelling of forest growth and yield has been an intrinsic part of forest research for more than 200 years but remains an area of active research. Growth models are necessary tools for simulating silvicultural options and different harvesting regimes in relation to forest research and forest management planning. The information so obtained may help forest practitioners and researchers to examine different alternatives in a cost effective way. The ability to make reasonable forecasts is especially important in forestry, where all effects of specific treatments may not be visible in the lifetime of the forester.

Forest growth models may operate on many different levels depending on the specific objective. Forest managers may require information on the present and future state of the forest, estimates of the maximum sustainable harvest, or want to forecast the timing and value of future harvests. On higher levels of detail, forest researchers, biologists or ecologists may need much more detailed information on forest development, for instance for simulating the ongoing conversion to near-natural forest management. Such information may be obtained from detailed measurements of the present forest structure, including information on individual trees, their spatial arrangement, ecological gradients etc. and a model suited for predicting individual-tree growth.

In the present study several growth models for European beech (*Fagus sylvatica* L.) in Denmark are developed from a large data-base of measurements from permanent sample plots. The database contains measurements from more than 1,600 measurement occasions on 69 individual experiments and 204 individual plots. The total database from the selected plots contains about 300,000 diameter and 35,000 height measurements of individual trees although not all these measurements were included in each particular modelling effort.

The work is presented in six individual manuscripts, five of which are submitted or accepted for publication in peer-reviewed, international forest research journals. The six manuscripts are found in the Papers-section of this dissertation and are:

- *Developing dynamic site index curves for European beech (Fagus syl-*

vatica L.) in Denmark. Accepted for publication in Forest Science.
(Paper I)

- *A state-space approach to stand growth modelling of European beech.* Submitted for publication in Forest Ecology and Management.
(Paper II)
- *A diameter distribution model for even-aged European beech in Denmark.* Submitted for publication in Forest Ecology and Management.
(Paper III)
- *Modelling individual-tree growth from data with highly irregular measurement intervals.* Accepted for publication in Forest Science.
(Paper IV)
- *Quantifying size-asymmetric growth among individual beech trees.* Accepted for publication in Canadian Journal of Forest Research.
(Paper V)
- *"A spatially explicit individual-tree model"*
(Paper VI)

The last manuscript (Paper VI) is not intended for publication in a scientific journal, but presents the results from a preliminary study on spatial individual-tree models and highlights some of the problems of spatial growth models and outlines the scope for future research in this area.

Site index model

Classification of forest land provides the basis for predicting expected yields of forest crops. In a study of dominant height-age curves, the development of a dynamic, base-age invariant site index model for beech in Denmark is presented. Derivation of the site index equations are based on the generalized algebraic difference approach (GADA), and the parameters of the model were estimated with correction for first order serial correlation. This approach used only tenable statistical assumptions and provided a significant improvement to the distribution of residuals compared to base-age specific models. Further, the base-age invariant method evaded the need for prior information on site index, which allowed efficient use of the available data. The resulting site index curves are polymorphic with variable asymptotes and may be used for estimating site index or predicting height growth from one or more observations of age and dominant height.

Stand growth model

Stand-level growth models are important tools for both forest managers and researchers as necessary information can easily be obtained in the forest to make predictions of future yield, expected revenues, or expected demands for machine or man power. The classical form of stand-level models - the yield table - fail to recognise that forest stands are dynamic systems, subject to sudden changes caused by silvicultural interventions.

Based on the state-space approach, a dynamic stand-level model of dominant height, basal area, and stem numbers was developed. The initial model uses a parameter estimate as an indicator of site quality, but also allows the use of site index for expressing the effect of site. The stand-level model may be used in simulation studies at stand level or for making local yield tables.

Diameter distribution model

Bridging the gap between crude stand-level simplifications and complex individual-tree models, diameter distribution models are potent tools for providing more detailed knowledge on the forest structure, product mix, product value, and forest operations costs for forest managers and researchers, without additional costs to obtain inventory data. A diameter distribution model was developed for even-aged monospecific beech stands. The model was based on the three-parameter Weibull distribution, and was estimated by non-linear fitting of the cumulative density function (cdf). Further, a model constrained to yield estimates consistent with observed basal area was estimated.

Predicted distributions were concordant with the expected development of diameter distributions in even-aged beech stands. However, a large number of predicted distributions deviated significantly from the observed in young stands and hence care should be taken when the model is applied to stands younger than 40 years.

Individual-tree growth models

In Denmark, increasing focus on silvicultural regimes that meet the demands for ecological, social, as well as economic goods has lead to the ongoing conversion towards near-natural or uneven-aged forestry. This paradigm shift in management of natural resources have created a demand for individual-tree growth models, able to model the conversion and the much more diverse forest structures expected in the future. Non-spatial models for predicting individual-tree diameter and height growth and mortality were developed for even-aged beech in Denmark. Fitting of the models to data with irregular measurement intervals required special consideration to the interpolation

of the independent variables. The study presented an iterative method for continuously updating individual-tree and stand-level attributes, using the hypothesized functional form of a system of forward difference equations.

In another study of the competitive interactions among individual trees, competition among n individual trees were simulated by n simultaneous differential equations. This allowed for explicit real-time modelling of plant interactions, which intuitively represents an improvement compared to the above described iterative approach to modelling individual-tree growth. By assuming that the growth of an individual within the population is a function of its size to a power a , a measure of the growth advantage of larger individuals (size-asymmetric growth) is provided. Since a provides a measure of the relative importance of above- versus belowground competition, it may be useful in interpreting the growth dynamics of forest stands, and may provide an additional level of information for modellers of forest growth.

Whereas non-spatial individual-tree models are expected to perform relatively well in homogeneous stands, the increasing spatial heterogeneity of the near-natural regimes may cause the non-spatial models to break down. A preliminary study was conducted to evaluate the predictive performance of a series of spatial and non-spatial models. Similarly to a number of other studies, the spatial models did not improve predictions. This result was discussed in relation to the spatio-temporal error structure of such models and the perspectives for future research on spatial individual-tree growth models were outlined.

Perspectives

The models presented in this dissertation serves a wide range of applications in forest management and research. However, the data underlying the models were essentially even-aged and monospecific, which ultimately limit the applicability of the models for simulating the more heterogeneous stand structures of near-natural forestry. Furthermore, the models did not include multiple sources of stochasticity inherent in the data and originating from variable, unobserved environmental factors such as climate. Hence, there remains a need for collecting growth and yield data from uneven-aged stands and a considerable scope for further research on the development of growth models for management of uneven-aged, mixed-species forests.

Dansk resumé

Udviklingen af modeller der beskriver skovens vækst og produktion har udgjort et betydeligt element i skovbrugsforskningen i mere end 200 år og er selv i dag et aktivt forskningsområde. Forstlige vækstmodeller er nødvendige værktøjer til at simulere forskellige skovdyrkningssystemer og finder anvendelse i skovplanlægningen såvel som i skovbrugsforskningen. Modellernes forudsigelser kan anvendes af skovbrugets praktikere samt inden for forskningen til at undersøge alternative dyrkningsformer på en enkel og billig måde. Denne mulighed for at lave langsigtede prognoser er af særlig vigtighed inden for skovbruget, idet effekten af en ændret skovdyrkning ofte først kan konstateres efter meget lang tid. Således kan en ændringer i skovdyrkningspraksis i dag få omfattende følger for skovens produktion og indtjeningsmuligheder langt ud i fremtiden, uden at disse effekter vil kunne ”observeres” på anden vis end ved brug af vækstmodeller i simulationsstudier.

Forstlige vækstmodeller kan operere på mange forskellige niveauer afhængig af formålet. Skovbrugets praktikere kan have behov for information på bevoksningsniveau om skovens nuværende og fremtidige tilstand og produktion, estimater for det maksimale gennemsnitlige vedvarende udbytte eller for at forudsige størrelsen eller udbyttet af fremtidige hugster og disses tidsmæssige fordeling. Skovbrugsforskningen, økologer eller biologer kan derimod have brug for information af en højere detaljeringsgrad eksempelvis i forbindelse med simulering af den igangværende konvertering til naturnært skovbrug. Sådanne simuleringer kan udføres ved hjælp af detaljerede målinger af den nuværende skovstruktur, inklusiv målinger af de enkelte træer, deres inbyrdes placering, økologiske gradienter mv. og en egnet enkelttræ tilvækstmodel.

Denne afhandling præsenterer en række forstlige vækstmodeller for bøg (*Fagus sylvatica* L.) i Danmark. Vækstmodellerne er præsenteret bagerst i afhandlingen i form af seks artikler, hvoraf de fem er eller forventes publiceret i anerkendte skovbrugsfaglige tidsskrifter:

- *Developing dynamic site index curves for European beech (Fagus sylvatica L.) in Denmark*. Optaget til publikation i Forest Science. (Paper I)
- *A state-space approach to stand growth modelling of European beech*.

Indsendt til publikation i Forest Ecology and Management.
(Paper II)

- *A diameter distribution model for even-aged European beech in Denmark.* Indsendt til publikation i Forest Ecology and Management.
(Paper III)
- *Modelling individual-tree growth from data with highly irregular measurement intervals.* Optaget til publikation i Forest Science.
(Paper IV)
- *Quantifying size-asymmetric growth among individual beech trees.* Optaget til publikation i Canadian Journal of Forest Research.
(Paper V)
- *"A spatially explicit individual-tree model"*
(Paper VI)

Den sidste artikel (Paper VI) præsenterer resultaterne af et indledende studie af afstandsafhængige enkelttræ tilvækstmodeller. Dette manuskript er ikke tænkt til at publiceres i et videnskabeligt tidsskrift, men behandler nogle af problemerne i forbindelse med udviklingen af afstandsafhængige modeller og perspektiverne for den fremtidige forskning på dette område.

De enkelte modeller er udviklet på grundlag af et stort forsøgsmateriale fra permanente prøveflader. Databasen indeholder målinger fra mere end 1,600 opgørelser af 69 forskellige forsøg med 204 individuelle parceller. Den samlede database indeholder mere end 300,000 diametermålinger og mere end 35,000 højdemålinger.

Bonitets kurver

Klassificering af skovjord til forskellige boniteter udgør grundlaget for de fleste forstlige vækstmodeller. I afhandlingen præsenteres udviklingen af et sæt af dynamiske bonitetskurver, der viser sammenhængen mellem højden af de dominerende træer og bevoksningsalderen. Udviklingen af bonitetskurverne er baseret på en såkaldt "generalized algebraic difference approach" (GADA), som sikrer konsistente estimater af højde og bonitet. Modellen blev estimeret med korrektion for første-ordens autokorrelation. Denne tilgang til udviklingen af bonitetskurver medførte betydelige forbedringer i forhold til tidligere tilgange til problemstillingen, idet estimationen ikke kræver et forudgående estimat for boniteten af de bevoksninger der indgår i estimationen af modellen. Herved sikres det at alle målte bevoksninger kan indgå i estimationen ligesom problemer med usikkerhed på estimatet af bonitet undgås.

Bevoksningsmodel

Modeller på bevoksningsniveau er vigtige værktøjer for såvel skovbrugets praktikere som for skovbrugsforskningen idet den for modellen nødvendige information enkelt og billigt kan indsamles i skoven og anvendes til at forudsige fremtidig produktion, forventede indtægter eller det forventede forbrug af maskiner og mandskab. Den klassiske form for bevoksningsmodeller - tilvækstoversigten - repræsenterer imidlertid kun et enkelt udviklingsforløb for en given bonitet, nemlig det forløb der ligger til grund for oversigten. Således tager tilvækstoversigten ikke hensyn til at den forstlige behandling ofte afviger fra den foreskrevne eller at naturskabte forandringer (f.eks. stormfald) grundlæggende kan ændre forudsætningerne i modellen.

Baseret på den såkaldte "state-space approach" er der i afhandlingen udviklet en dynamisk bevoksningsmodel for overhøjde, grundflade og stamtal. Det dynamiske element ligger i at funktionerne kun behøver den nuværende bevoksnings tilstand for at kunne forudsige tilvæksten i det kommende år. Informationen om den fremtidige vækst findes altså i den nuværende bevoksningsstilstand. Modellen anvender et lokalt estimat af en parameter som indikator for lokalitetens produktionsevne, men tillader at bonitet (overhøjde ved alder 50) bruges istedet. Bevoksningsmodellen kan bruges til at simulere udviklingen i konkrete bevoksninger eller som hjælpemiddel til at udvikle lokale tilvækstoversigter.

Diameter-fordelingsmodel

Modeller der beskriver fordelingen af træer til forskellige størrelser ud fra bevoksningsvariable som overhøjde, grundflade, diameter eller stamtal er et kraftfuldt værktøj for skovdyrkere og forskere til at skaffe mere detaljeret viden om den forventede skovstruktur, sortimentsudfald, værdien af tyndinger eller skovningsomkostninger uden at øge omkostningerne til indsamling af taksations data. En diameter-fordelingsmodel for ensaldrende bølgebevoksninger er præsenteret i afhandlingen.

Modellen er baseret på en tre-parameter Weibull fordeling. Modellens parametre blev estimeret simultant som funktioner af stamtal, grundflade og diameteren af det grundfladevejede middeltræ. Yderligere blev modellen estimeret i en form der sikrer overensstemmelse med den observerede grundflade. De non-lineære modeller blev estimeret ved at minimere afvigelses kvadrater mellem den observerede og predikterede kumulative hyppighed.

De estimerede diameterfordelinger var i overensstemmelse med den forventede udvikling af størrelsesfordelingen i ensaldrede bølgebevoksninger. På baggrund af de statistiske analyser af de predikterede fordelinger stod det imidlertid klart at modellen, særligt i unge bevoksninger (<40 år) ofte afveg fra den observerede fordeling. Dette skyldes formentlig store forskelle i

stamtal på anlægstidspunktet og betyder at modellen skal anvendes med varsomhed i unge bevoksninger.

Enkelttræmodeller

Det øgede fokus på skovdyrkningssystemer der imødekommer efterspørgslen efter økologiske, sociale og økonomiske goder har i Danmark ledt til den igangværende konvertering til naturnært skovbrug. Dette paradigmeskift i naturresourceforvaltningen har skabt efterspørgsel efter vækstmodeller på enkelttræniveau, der bedre end bevoksningsmodellerne er i stand til at modellere de mere uensartede skovstrukturer, der er den forventede konsekvens af den ændrede skovdyrkning.

I afhandlingen præsenteres en afstands-uafhængig enkelttræmodel der beskriver mortalitet samt diameter- og højdetilvækst for ensaldrende bøg i Danmark. Estimationen af parametrene i den dynamiske model krævede særlig hensyntagen til normaliseringen af data, som var indsamlet med forskellige intervaller. Modellernes parametre blev derfor estimeret ved en iterativ procedure, hvor ikke-observerede værdier af de uafhængige variable mellem målinger beregnedes ud fra et første gæt på modellens parametre. Ud fra disse værdier estimeredes nye parametre for modellen, der så igen blev brugt til at beregne de mellemliggende værdier af de uafhængige variable. Denne procedure blev gentaget indtil modellen konvergerede.

Enkelttræ-modellen producerede relativt præcise estimater af den gennemsnitlige tilvækst, selvom de årlige variationer er ganske store. Modellen kan enkelt anvendes ved simulering af enkelttræ-tilvækst i studier af specifikke hugstsystemer som f.eks. måldiameterhugst.

Den iterative metode til estimation af enkelttræ-tilvækstmodeller er i afhandlingen forbedret i et studie af konkurrencen mellem enkelte træer, hvor træernes vækst og interaktion blev simuleret simultant ved n individuelle differential-ligninger for de n træer. Dette tillod træerne i modellen at interagere mere naturligt og ses som en væsentlig forbedring i forhold til tidligere estimationsmetoder. Imidlertid er denne metode yderst krævende mht. computer-capacitet (estimationen af modellen på blot 100 træer tog næsten en måned på en kraftig PC), og er derfor endnu ikke anvendelig til estimation af generelle enkelttræ-modeller baseret på større mængder af data.

Imens afstands-uafhængige modeller forventes at klare sig relativt godt i ensaldrende bevoksninger, er det straks mere tvivlsomt hvorvidt disse modeller kan forventes at give rimelige resultater i mere uensartede skovstrukturer, der er den forventede konsekvens af konverteringen til naturnært skovbrug. Et indledende studie af afstands-afhængige enkelttræmodeller er

gennemført i afhandlingen for at evaluere disse modellers prædiktionssevne i forhold til den afstands-uafhængige model. I lighed med en række tidligere studier var resultatet nedslående idet inddragelsen af træernes indbyrdes placering ikke gav anledning til forbedrede prædiktioner. Dette resultat diskuteres i afhandlingen i forhold til de underliggende antagelser om variationen inden for skovbevoksninger og i relation til den fremtidige forskning indenfor udviklingen af afstands-afhængige enkelttræ modeller.

Perspektiver

De forskellige modeller der præsenteres i afhandlingen kan anvedes på en lang række forstlige problemstillinger inden for skovbrugsplanlægning eller -forskning. Imidlertid repræsenterer det underliggende data langt overvejende ensaldrende bevoksninger med kun én træart. Således kan man stille spørgsmål ved i hvilket omfang modellerne er i stand til at simulere den igangværende konvertering til naturnært skovbrug. Ydermere er der fortsat betydelige perspektiver for at forbedre metoderne til estimation af enkelttræ-vækstmodeller. Der eksisterer således stadig et behov for indsamling af data fra uensaldrende, blandskovsbevoksninger og for at udvikle nye metoder til at estimere modeller for sådanne bevoksninger.

Contents

Preface	iii
Summary	v
Site index model	vi
Stand growth model	vii
Diameter distribution model	vii
Individual-tree growth models	vii
Perspectives	viii
Dansk resumé	ix
Bonitets kurver	x
Bevoksningsmodel	xi
Diameter-fordelingsmodel	xi
Enkelttræmodeller	xii
Perspektiver	xiii
1 Introduction	1
1.1 Research objectives	2
1.2 European beech	2
1.2.1 Geographic distribution	3
1.2.2 Development of modern forest management practises .	6
1.2.3 Current beech management	8
1.2.4 New trends - towards sustainable forest management .	10
2 Data	13
2.1 Measurements	13
2.2 Calculations	16
2.3 Data ranges	16
3 Modelling growth of beech in Denmark	21
3.1 Assessment of site quality	22
3.1.1 Determining site quality	23
3.1.2 Estimating site index curves for European beech in Denmark	25

3.1.3	Application of the site index curves	27
3.1.4	Estimation of the height of the mean basal area tree from dominant height	27
3.2	Stand-level growth models	29
3.2.1	A dynamic stand-level growth model for beech	33
3.2.2	Application of the dynamic stand-level growth model .	37
3.3	Size-distribution models	39
3.3.1	A diameter-distribution model for beech	41
3.3.2	Application of the diameter-distribution model	43
3.4	Individual tree growth models	44
3.4.1	A non-spatial individual-tree growth model	46
3.4.2	Quantifying individual-tree competition	53
3.4.3	A spatial individual-tree growth model	56
3.4.4	Application of the non-spatial individual-tree model .	57
4	Conclusions and perspectives	59
	Bibliography	60
	Papers	85
I	Developing dynamic site index curves	85
	Introduction	87
	Materials	89
	Methods	91
	Results	94
	Discussion	97
	Conclusion	103
	Acknowledgements	103
	Literature cited	103
II	A state-space approach to stand growth modelling	107
	Introduction	109
	Materials	110
	Methods	111
	Model description	113
	Site-specific effects	114
	Model estimation	115
	Statistical fit of the model	117
	Results	118
	Discussion	121
	Conclusions	126
	References	126

III A diameter distribution model for even-aged beech	131
Introduction	133
Materials	135
Methods	136
Model estimation	136
Model evaluation	142
Results	143
Discussion	145
Conclusion	149
References	149
IV Modelling individual-tree growth	155
Introduction	157
Data	159
Methods	160
Model estimation	162
Error structure	164
Site-specific effects	165
Model evaluation	166
Results	167
Discussion and conclusions	174
Acknowledgements	177
Literature cited	177
V Quantifying size-asymmetric growth	183
Introduction	186
Materials and methods	187
Data collection	187
Model description	188
Model estimation	191
Statistical fit of the model	192
Results	192
Discussion	195
References	197
VI A spatially explicit individual-tree model	203
Introduction	205
Materials	206
Methods	206
Results	210
Discussion	210
Literature cited	213

Appendices	219
A Examples of yield tables for beech	219
B The experiments	223

Chapter 1

Introduction

Models of forest growth have been an intrinsic part of forest research for more than two centuries. As early as in 1793 Reventlow (1879, pp. 5-154)¹ conducted stem analyses on felled oaks and beeches in his forests on Pederstrup and Christianssæde on the island Lolland. During the following years, similar analyses were made in the Royal Danish forest districts Copenhagen, Hirschholm, and Kronborg and the forests belonging to Sorø Academy and Petersgaard. The data so collected were unique by the scientific standards of the time and made it possible to calculate annual increment of individual trees and to assess its dependence on age, tree size and the spatial distribution of the trees. Since the ground-breaking work of Reventlow, literally thousands of models for predicting forest growth have been published, although it took almost hundred years before the advanced modelling of individual-tree growth suggested by Reventlow was adopted by other researchers (e.g. Lemmon and Schumacher, 1962a; Spurr, 1962; Newnham and Smith, 1964; Opie, 1962; Bella, 1971; Daniels, 1976).

Simulation of different silvicultural options and harvesting regimes using growth models represents a cost-effective way to examine various management alternatives for forest practitioners and researchers. With suitable data, growth models may help determine sustainable timber yield, examine the economics of alternative silvicultural regimes, provide valuable insight into the impact of forest management interventions on forest structure and growth, or help assess the effects of forest management on other values produced by the forest (i.e. recreational or biological values). The ability to make reasonable forecasts is especially important in forestry, where the effects of specific treatments may not be visible in the lifetime of the forester.

¹Reventlow wrote "Forslag til en Forbedret Skovbehandling grundet på Undersøgelser over Træernes Vegetation i Danmarks og Slesvigs Skove" (in English: "Treatise on Forestry") during the years 1800-1827 in Danish and later in German. However, due to financial problems the manuscript was not published until 1879, when his granddaughter Countess B. Reventlow financed the publication of the Danish manuscript edited by W. Gyldenfeldt.

Hence the long term effects of forest management cannot be evaluated by personal experience alone.

Forest growth models have been developed at different scales of resolution and the appropriate model depends on the the specific application. Forest managers may require information on the present and future status of the forest, estimates of the maximum sustainable harvest, or forecasts of the value of future harvests. Such information may be compiled from stand-level inventory data and suitable stand-level growth models.

The stand-level estimates of present and future status of the forest represent crude simplifications of the forest structure, but represent valuable information for the experienced forester. However, information may be further detailed by allocating stand-level estimates to different species and size classes. Such information is valuable when forecasting the assortment distribution and value of future harvests and may be obtained by applying size-distribution models to the stand-level estimates.

Forest researchers, biologists or ecologists may need much more detailed information on forest development, for instance for simulating the ongoing conversion to near-natural forest management. Such information may be obtained from detailed measurements of ecological gradients within the stand, the present forest structure, including information on individual trees and their spatial arrangement and a model suited for predicting individual-tree growth. Such information is far too detailed and costly to obtain for forest practitioners and such models are of little value to them, but individual-tree models provide valuable insight into the ecological functions of the forest and detailed information on expected stand development.

1.1 Research objectives

European beech is the most common deciduous species in Denmark and also one of the most important ones in economic terms. Despite the importance of this species, available models for beech forest management planning and research in Denmark are at present limited to yield tables for even-aged monocultures. Hence, the objective of this study is to develop growth models for various applications in forest management and research, and to demonstrate their application. Based on the findings of the study, the scope for future research within forest growth and yield modelling is discussed.

1.2 European beech

European beech or common beech (*Fagus sylvatica* L.) belongs to the family Fagaceae. *Fagus* comes from a Greek word meaning 'to eat,' referring to the edible mast. Beech is a tall deciduous forest tree, reaching over 40 m in

height on good sites, with a straight, sturdy trunk. It has smooth grey bark and a broad dense crown (Figure 1.1).

European beech is one of the most common forest tree species in central and northern Europe. Covering 17% of the total forest area it is the most common deciduous species in Denmark (Larsen and Johannsen, 2002, pp. 17-54) and also one of the most significant ones in economic terms. The wood has excellent elasticity and strength properties and its homogeneity, lack of odour and taste and excellent workability makes it suitable for many applications. In a historical perspective a large proportion of the harvest volume was used for firewood, tool making, containers for butter and meat and wooden shoes. Wood for making shoes alone accounted for an annual consumption of 45,000 m³ in 1918 (Moltesen, 1988, pp. 72-74). A large proportion of the beech wood was used as sleepers for the railroads from 1930, but this market has almost been taken over by concrete sleepers. Today the beech wood is being used for firewood, parquet floors, veneer and semi-manufactured products for the furniture industry (Table 1.1).

Table 1.1: Annual harvest volumes in m³ over bark from 1994 to 2003 in Denmark (Statistics Denmark, 2006).

	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
Harvest volume	4761	4883	4758	4641	4139	4163	4905	3143	2542	2439
Timber	3131	3258	3035	2960	2555	2623	3204	1588	1107	827
Firewood	1606	1603	1697	1643	1534	1503	1648	1512	1412	1613
Wood-chips	24	22	26	38	50	37	53	43	23	.

1.2.1 Geographic distribution

About 16,000 years ago the latest of a series of ice ages, the Weichsel glaciation, came to an end. The glaciers that covered most of Denmark except for south-west Jutland withdrew and revealed a tree-less land shaped by the ice. The warmer climate allowed the spread of higher plants and 2,000-3,000 years after the end of the glaciation, willow, birch and poplar species formed a tundra landscape. As the climate became warmer other, less tolerant species appeared and pollen analyses show distinct periods where the landscape was dominated by pine, hazel and lime (Hannon et al., 2000). The relatively less frost tolerant beech spread to Denmark during the Bronze Age 1,000-2,000 BC.

In the current climate, European beech is native to northern and central Europe and thrives in the mild Atlantic climates (Figure 1.2). To the north and east, the distribution of beech is limited by the cold continental climate. Although the species tolerates cold winters, catastrophic frosts with temperatures below -35°C leads to withering of the crown and death of entire stands. More importantly, late frosts severely affect the quality of



Figure 1.1: European beech (Photo: Morten Christensen).

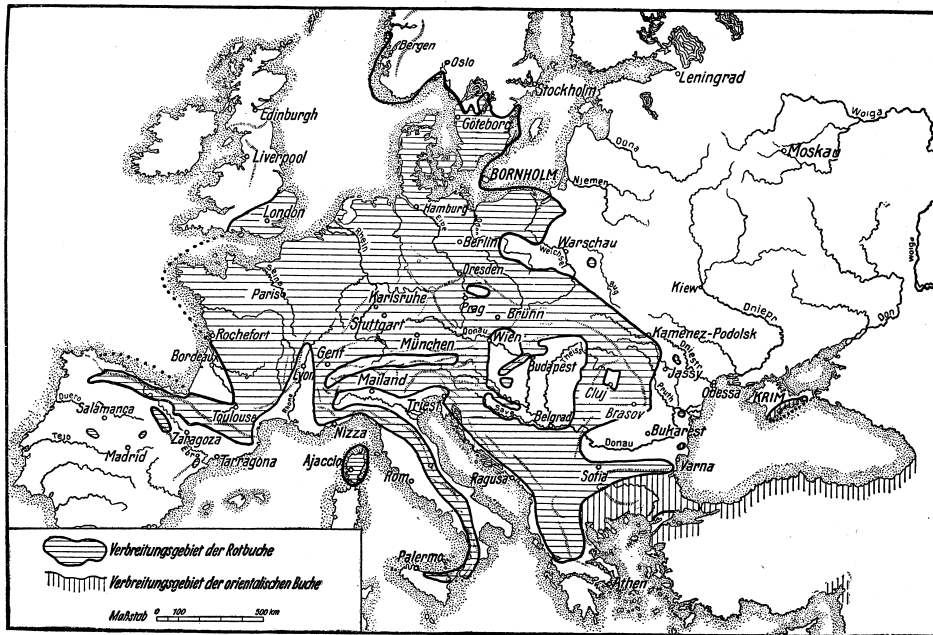


Figure 1.2: The area of distribution for European beech. Copied from Rubner (1960, p. 443, plate 118).

the beech mast, which has decisive impact on northern distribution of beech (Oppermann and Bornebusch, 1926; Lindquist, 1931). Also the growth of young beech trees is severely affected by late frosts, which affect their ability to compete with other species and hence restricts the species northern and eastern distribution (Hauch, 1908; Rubner, 1921; Lindquist, 1931). To the south and east the area of distribution of beech seems to be limited by drought during the growing season (Rubner, 1960).

In Denmark beech is close to the northern limit of its distribution and it thrives in the cool, temperate climate. Beech is a climax species and it often forms mono-specific stands as a result of its broad, dense crown that shades away competing vegetation, and the shade tolerance of beech seedlings. In virgin deciduous forests, beech is considered a predominant element in a mosaic cycle between different developmental phases. In the near-natural forest Suserup Skov in eastern Denmark five distinct developmental phases were identified: regeneration, aggradation, early bio-static, late bio-static, and degradation (Emborg et al., 2000). During the first phases the canopy layer of gaps generated by dying or fallen trees are dominated by ash (*Fraxinus excelsior* L.) because of its properties as a pioneer species, spreading lots of wind-dispersed seeds and its rapid vegetative development. During these early phases, the lower stratum of the canopy is dominated by the

shade tolerant beech. As the early bio-static phase begins dominant ash trees begin to show increasing senescence and during this phase the canopy layer is completely taken over by beech. New gaps are formed after 250-300 years when the dominant trees die during the degeneration phase. In a spatial context the result is a shifting mosaic, where the individual phases are taking place in different parts of the stand (Emborg, 1998).

1.2.2 Development of modern forest management practises

Until the industrialisation, the forest resource had tremendous importance. The wood was used for a wide variety of purposes: firewood for heating and cooking, wood for fencing, tool making, and shoes, and timber for building houses and ships. Further, the forests were used for hunting, grazing and for picking berries and nuts. In spite of the importance of the forest resource, early forest "management" in Denmark may best be characterised as non-managed utilization of the forest resource and the forests were exclusively regenerated by spontaneous natural regeneration.

From the 1200-years there is evidence of merging legislation for the utilization of the forest resource, although the predominant guideline for the activities was to "cut the trees where it caused the least damage to the forest" (Oppermann, 1887, p. 10). At this time the rights to use the timber producing species became limited to the higher classes of society (Fritzbøger, 1994, pp. 315-319). This right was affirmed with the Forest Act of 1670 that stated that all beech, ash and oak trees were reserved for the upper classes. However, the lower classes had the rights to use the lower storey trees for firewood, fencing and construction and to let livestock feed on the foliage and mast. This led to conflicting goals of forest management since the lower classes had no motivation to let the forest develop into high forest, which would ultimately reduce the production of their resources. Combined with an ever increasing population and hence, increasing demands for firewood and construction timber this led to depletion of the forest resource.

From the beginning of 1500 AC there is increasing evidence of scarcity of forest resources. Not only were forests decreasing in number and size but the remaining forests were increasingly open with few very old trees and grass-grown forest floor that impeded the natural regeneration. To illustrate the poor state of the forests the average volume of the forests in northern Zealand was 143 m³/ha in 1766 (Oppermann, 1887, pp. 12-13). In the beginning of the 1700-years the diminishing forest resource forced the crown to take action to secure the sustained production of wood. At the request of Carl Christian von Gram, who was Master of the Royal Hunt, the German forester Johan Georg von Langen was in 1763 asked to reform Danish forestry. Relying on new ideas from Hartz in northern Germany, he introduced forest planning, clear-felling and the concept of the "normal forest" in order to secure sustainable wood production.

The ideas of modern forest practises introduced by von Langen had far-reaching consequences for forest management in Denmark. He initiated extensive forest inventories of the forests in northern Zealand. Based on the inventories the forests were then divided into easily manageable units called compartments, each compartment having only one species of the same age. Also a number of other species were introduced to Danish forestry, such as Norway spruce (*Picea abies*), silver fir (*Abies alba*), European larch (*Larix decidua*), Scots pine (*Pinus sylvestris*), sycamore (*Acer pseudoplatanus*), horse chestnut (*Aesculus hippocastanea*) and sweet chestnut (*Castanea sativa*).

In the forest management introduced by von Langen, the compartments served as the basic management unit. The individual compartments were clear-felled at their rotation age, which was no more than 100 years, leaving only occasionally a few seed trees. At a few occasions a regeneration thinning was carried out to facilitate natural regeneration, but Gram noted that this was not successful (Oppermann, 1887, p. 14). In general the regeneration was made on the clear-felled area by planting in grooves four metres apart and with one metre between the plants. The wide spacing between the grooves allowed for hay harvest and some sort of agro-forestry to secure early returns from the forest stands. Later this method was widely abandoned and the forest was instead regenerated by strip sowing. According to the plan, the forest stands were thinned three times, combined with pruning of the stems, during the rotation.

Despite the increasing scarcity of forest resources and problems of sand drift on large areas, the ideas presented by von Langen was met with fierce resistance due to the tremendous costs incurred by his efforts. In 1770 von Langen became increasingly ill and followed the reformation of the forest from his sickbed until his death in 1776. In 1778 the reforms were abandoned entirely by the crown because of the costs and the work was deferred for 20 years. However, over the years the ideas of forest management and planning had spread to a number of private forests (Fritzbøger, 1994, pp. 273-280). Georg Wilhelm Brüel promoted the preparation of forest plans in Jutland and on the island Lolland. His work was noted by C.D.F. Reventlow and forest plans were prepared for the forests of Christianssæde and Pederstrup and later for the forests of Brahetrolleborg on Funen, where his brother J.L. Reventlow resided. When C.D.F. Reventlow became Director of the Exchequer in 1784 the reformation of the Danish forests and introduction of forest management planning initiated by von Langen gained renewed momentum for both private and state owned forests.

Despite the intentions of developing a sustainable wood production, the forest land was still under an immense pressure due to the historical rights to different parts of the forest resource. After a searing scarcity of firewood during the winter 1804-05, the government issued the Forest Reserve Act in 1805. The land was separated into protected forest land and agricultural

land and the partition of rights to different parts of the forest was abolished. At this point the forests covered only 3-4% of the land. In the remaining forests, inventories were carried out and forest plans prepared through the 1800-years for both private and state forests. The plan for the 19,432 ha of state forest was finished in 1804 and emphasized the high forest, clear-felling regime as the sole silvicultural system (Fritzbøger, 1994, pp. 273-280). The plan stated that the rotation age was to be 200 years for oak and 80 years for beech and further provided an economic assessment of expected income and expenses.

For more than a century the clear-felling regime remained the sole silvicultural system, successfully securing the sustainable production of wood. At the time of World War I, import of wood was hindered and Danish government demanded that the scarcity of wood was met by shortening the rotation age, and introducing heavy thinnings and compulsory fellings. As a reaction against what was viewed as destruction of the forest, a number of foresters advocated continuous-cover forestry. Based on the German "Dauerwald"-movement, they promoted the perception of the forest as a biological system rather than a mere production entity. The resulting forest would be uneven-aged and multispecific and clear-fellings were to be abolished entirely. However, their ideas were not generally accepted and the even-aged, high forest regime introduced by von Langen is even today by far the predominant silvicultural system in Denmark.

1.2.3 Current beech management

Although von Langen never lived to see his ambitious plans carried out, the ideas that he introduced have shaped forests and forest management practises in Denmark for more than two centuries. Also today's management of beech forests in Denmark is strongly influenced by von Langens ideas although some modifications are made to his management regime.

Depending on the natural conditions, beech forests are often regenerated by natural regeneration that is sometimes initiated by a preparation thinning to stimulate seed formation. To ensure a complete regeneration a seedbed is often established by the use of a disk harrow and/or a mouldboard plough. After the seed fall, the beech nuts may be mixed into soil of the A-horizon by a more shallow soil preparation (Henriksen, 1988, pp. 150-173; Møller, 1965, pp. 21-22, 447-449). During the winter following a mast year (often occurring in the following year after a warm and dry summer (June and July; Holmsgaard and Olsen, 1960) a regeneration thinning is carried out to promote favourable light conditions and reduce the competition for water (Sabroe, 1967; Henriksen, 1988, pp. 150-152). In stands where the natural conditions are less favourable for natural regeneration e.g. due to heavy grass cover or when a beech stand is established where beech was not present before, the stand is established by planting. Today the plants are planted

at 1.25x1.25 m or 1.25x1.5 m corresponding to 6,400 or 5,300 plants per hectare but historically, planted stands were established at much higher densities (>10,000 plants per hectare Henriksen, 1988, p. 219).

In the years following natural regeneration, the competition from the old stand is gradually reduced by light thinnings. The liquidation pace is a fine balance between reducing competition for the beech seedlings while still hindering the formation of competitive vegetation (Sabroe, 1967). The extensive measures carried out to ensure a complete regeneration often result in very plant rich regenerations with literally millions of seedlings. To promote a more rapid diameter development, pre-commercial thinnings are often carried out by making rows using a tractor-mounted chipper (Madsen and Pedersen, 2002). Later pre-commercial thinnings are mostly carried out manually to promote the growth of the best-formed individuals, to secure the optimal spacing for their qualitative development, to promote the formation of a vital understorey and to secure the desired species composition.

Later thinnings are carried out to provide early returns and at the same time to promote the growth of high-quality trees without hampering future growth or the qualitative development of the stand as a whole. The fine balance between obtaining early returns by thinning while securing the future value of the stand has created much debate on the optimal thinning practise (Bornebusch, 1940; Møller and Holmsgaard, 1947; Henriksen, 1952; Abell and Jagd, 1954; Bryndum, 1980). Two opposing thinning strategies have dominated the debate on the optimal thinning in beech: a frequent regime of moderate thinnings referred to as "Danish thinning" and a regime of initial light thinnings until age 50-60 that is then accelerated and in old ages resemble that of the Danish thinning. The latter thinning regime is referred to as "Funen thinning" after the Danish island Funen.

The very first proponent of the Danish thinning was C.D.F. Reventlow, who in 1811 argued that substantially reducing the canopy cover would lead to increased merchantable volume production as well as total production (c.f. Grøn, 1931, pp. 491-492). As Reventlow adhered to the economic school of maximum net present value ("bodenreinertrag") rather than maximum sustained yield ("waldreinertrag"), his impatience regarding the returns from the forest investment also affected his strategy towards early, heavy thinnings (Grøn, 1931; Helles and Linddal, 1952). Later proponents of the Danish thinning have demonstrated that although total volume production is not increased by reducing the canopy cover it is widely unaffected within a wide range of densities. Further, current consensus support the notion that thinnings redistribute the increment from smaller to larger stems thus securing a larger amount of merchantable volume and shortening of the rotation age. For beech, the latter reduces the risk of red heart, which to some extent is dependent on age (Naumann and Julich, 1997) and often results in declassification of the stem and a significant economic loss.

Proponents of the Funen thinning regime advocate that early thinnings

should only be targeted at poorly shaped trees that hamper the growth of qualitatively better trees, thus leading to higher density compared to Danish thinning. They argue that although the average diameter of the stand may be negatively influenced by the higher density, the growth of the best performing trees is not affected nearly as much. When more stems are left in the stand the forester is also left with more alternatives when future crop trees are damaged or show less attractive qualitative development. Further, the relatively dense stand at young ages secures the early dying of lower branches and thus a longer bole and improved quality. The acceleration of thinning intensity later secures a rapid diameter development and shortens the rotation age without affecting the quality of the stand since epicormic branches rarely form on beech.

It seems that both arguments may be valid, depending on the preconditions (Bornebusch, 1940, Møller, 1965, pp. 24-25). In stands of general poor quality a heavy thinning regime like Danish thinning is certainly justified to promote the growth of the few qualitatively well-formed individuals. In a stand of better quality it may be more reasonable to seek the development of a long bole by applying a lighter thinning regime. It is therefore not surprising that many forest districts practise both thinning strategies, depending on the qualitative development of particular stands.

At the end of the rotation, liquidation of the stand has been almost as fiercely discussed as the thinning practise (Petersen, 1967, 1981, 1982; Holten-Andersen, 1986). Historically the rotation age for beech has been around 120 years in most forest management plans (Møller, 1965, pp. 30-31, Henriksen, 1988, p. 533). The rotation age is however largely dependent on the thinning regime, the risk of red heart and the economical situation of the forest owner. Due to the high cost of planting, analyses indicate that cyclic rotations of naturally regenerated beech may be economically superior to clear-felling regimes (Petersen, 1982; Holten-Andersen, 1986; Nord-Larsen et al., 2003). Therefore most beech stands are naturally regenerated with a regeneration thinning around age 90 years and gradual liquidation of the holdover during the following 20 years, depending on the development of the regeneration.

1.2.4 New trends - towards sustainable forest management

The concept of sustainability, as defined by the Brundtland Commission in 1987 (WCED, 1987), and the world summit on environment and development in Rio in 1992, has created a widespread interest for the introduction of silvicultural regimes that meet the demand for ecological, social as well as economic benefits. Based on the conclusions of the World Summit in Rio and subsequent national work (Skov- og Naturstyrelsen, 1994) the Danish Ministry of Environment published the National Forest Programme in 2002 (Skov- og Naturstyrelsen, 2002). The National Forest Programme empha-

sized that forest management practises based on the natural processes of the forest ecosystem enables the development of a sustainable forestry that protect the ecological structures and functions, as well as satisfies the economic needs of the forest owner. The philosophy behind this "near-natural" stand management is to adopt silvicultural principles in accordance with the ecological processes in the forest and let them merge with economic rationality (Holm, 1979; Larsen, 1997). The recommendations of the National Forest Programme were implemented by the Action Plan for the conversion of all state forests to near-natural forestry (Skov- og Naturstyrelsen, 2005; Skov- og Naturstyrelsen and Larsen, 2005a,b).

To facilitate the transition from the present silvicultural regimes to near-natural forest management, principles of near-natural stand management has been formulated as 13 operational guidelines (Anonymous, 2001; Larsen and Madsen, 2001). In short, the guidelines aim to secure the long-term productivity, ecological functionality and the biodiversity by: 1) omitting clear-cuts and promoting productive, site-adapted tree species that secure soil fertility, 2) securing natural regeneration and promoting species mixtures through a forest management that enhances the forest climate and support natural ingrowth of other tree species, 3) development of uneven-aged forest stands by utilization of natural successions which supports the development of structural variation, such as natural selection and harvesting by target diameter and 4) omitting the use of pesticides and fencing by using tree species which are not dependent on protection, using regeneration and biotic methods suitable to control pests, enforcing ecosystem-adapted game management and use of ecosystem adapted harvest and regeneration techniques that protect the forest stand as well as the site.

As beech is a dominant element of most natural forest ecosystems in Denmark it will play a major role in the development of the near-natural forestry. Conversion of even-aged, monospecific beech stands to uneven-aged, heterogeneous, mixed-species structures of near-natural forestry may be done by changing from the traditional thinning from below to selection thinning mostly from above (Skov- og Naturstyrelsen and Larsen, 2005a). Harvesting according to individual maturity criteria leads to prolonged retention of qualitatively excellent trees and to some degree mimics the dynamics of natural beech forests (Christensen and Emborg, 1996). Further, harvesting according to target diameter reduces the need for homogenising the stand prior to harvest since the trees are felled according to individual maturity criteria and not the maturity of the average tree of the stand. This allows for expansion of the diameter distribution within the stand, which in turn broadens the time span of the liquidation of holdovers and causes differentiated suppression of the regeneration. The result is a process that further enhances the diversity of tree sizes.

The success of the conversion depends on the establishment of regeneration in the gaps as canopy trees are removed. In younger stands, where

the dense canopy layer effectively intercept the sun and thus prevent the development of competing vegetation, regeneration will probably be successful without further measures. However in old, heavily thinned stands where grass has covered the forest floor, subsequent planting may be necessary to successfully regenerate the stand and to secure the development of mixed-species stands.

Conversion to near-natural forestry is no new invention but has been an active part of the debate on development of forestry for several hundred years. However, attempts to introduce such forestry have often resulted in devastation of the forests because forestry based on the individual tree has excluded efficient planning of the utilization of the forest resource. In 1888, Oppermann (p. 10) notes that "recent developments towards uneven-aged forestry should bare in mind that this type of forestry was contributing to the devastation of Danish forests only 100 years ago". A similar warning was issued by Hauch in 1921. Also attempts to introduce near-natural forestry in Sweden around 1900 lead to deprivation of valuable forests and was later referred to as "the green lie" as many felt that near-natural forestry was merely an excuse to rob the forest of any value. This type of forestry was banned during the 1950's as it was considered a threat to the continued production capability of the Swedish forests. To me it appears that the failure of near-natural forest management to represent a viable alternative to the traditional management has mainly been due to the lack of suitable planning tools. The development of new and better suited tools for managing the diverse structures of near-natural forest will therefore be a task of great importance in the years to come, particularly now that the number of employees in most forests has decreased drastically.

Chapter 2

Data

The data for modelling the growth of European beech in Denmark originate from 69 permanent spacing, species and thinning experiments including 201 individual plots and a total of 2018 measurement occasions. Detailed information on the individual experiments is provided in Appendix B. Plot sizes vary between 0.07 and 2.65 ha with an average of 0.40 ha. The experiments are located in most parts of Denmark and cover a wide range of site conditions (Figure 2.1). However, the majority are situated in the eastern parts of the country where the growth conditions are more suitable for growing beech than on the sandy soils in western Denmark.

2.1 Measurements

The data were collected during the period from 1872 to 2005 and the stands were observed for 10 to 120 years (Figure 2.2). Despite the long time span, data collection on the permanent sample plots has been remarkably uniform. In the earliest measurements diameter readings were taken at 1/20 tree height. After 1880 trees were generally marked permanently at 4.15 feet (~ 1.3 m), numbered and recorded individually. In some cases however, trees were recorded in tally list to 1-inch diameter classes.

The conversion to the metric system in 1902 had little influence on the measurement practises except that trees were now recorded in tally lists to 1-cm rather than 1-inch diameter classes. Consequently, the data used for modelling growth and yield represents more than 120 years of consistent measurements.

Measurements of diameter were obtained by averaging two perpendicular calliper readings taken at breast height (1.3m) for each tree. Observations also included records on whether the tree is alive or dead at the time of measurement. The height of live trees was measured using a hypsometer and felled trees were measured on the ground using a tape measure. On average 32.9 tree height measurements were obtained per measurement occasion.

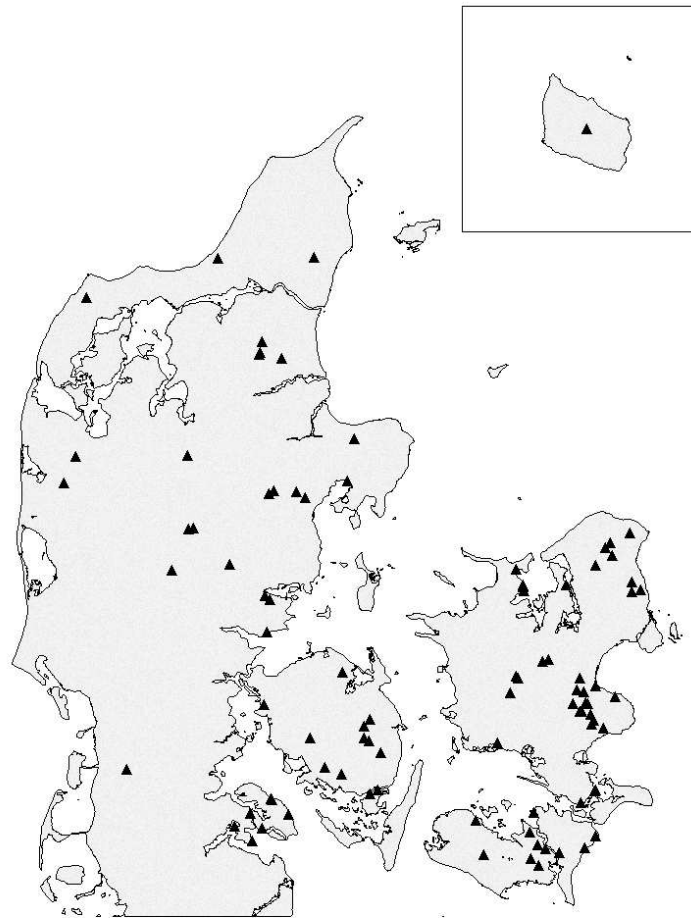


Figure 2.1: The location of Danish beech experiments included in the present study.

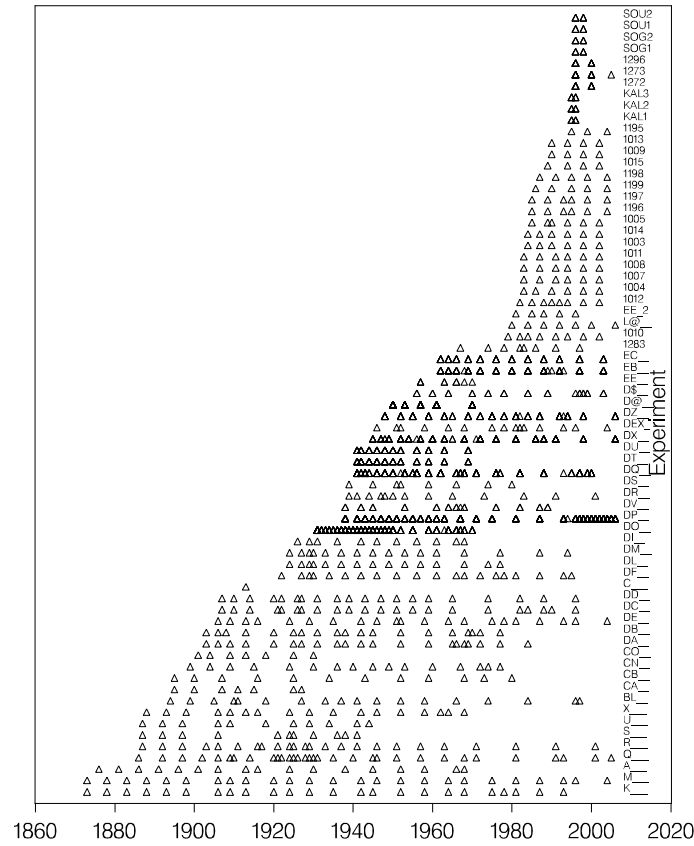


Figure 2.2: Illustration of measurements carried out in the stands included in the modelling of individual-tree growth. Triangles indicate each measurement occasion.

In 20 plots from 16 permanent thinning experiments, individual-tree positions were recorded ¹. These experiments were all located in the eastern parts of Denmark. In 48 experiments soil texture analyses were carried out, providing information on fractions of clay, silt, fine sand and coarse sand in the top one metre of the mineral soil.

2.2 Calculations

Stem numbers, N (ha^{-1}), were calculated as the number of individual trees per hectare taller than 1.3 m. When trees forked below 1.3 m, each stem was measured individually but multiple stems from the same root were counted as one tree. Within the research plots, trees were typically separated into over- and understorey and the understorey was measured less intensively than the overstorey.

Stand basal area, G ($\text{m}^2 \text{ha}^{-1}$), of each plot was estimated by summation of individual-tree basal areas calculated from the diameter measurements. When trees were recorded in tally lists, the middiameter of each class was used as an estimate of the diameter of all trees in that class. Diameter of the mean basal area tree, D_g (cm), was derived from the estimates of N and G .

Based on paired observations of diameter and height, height-diameter equations were estimated for each plot and measurement combination using a modified Näslund-equation (Näslund, 1936; Johannsen, 2002):

$$h = 1.3 + \left(\frac{d}{\alpha + \beta \cdot d} \right)^3 \quad (2.1)$$

where d is the diameter at breast height, h is the total tree height and α and β are parameters to be estimated. The equations were then used to estimate the height of trees not measured. Dominant height, defined as the mean height of the 100 thickest trees per hectare (H_{100}), was then calculated for each plot and measurement combination. In the few cases where stem numbers were less than 100 per hectare, H_{100} was estimated as the mean height. Height corresponding to average basal area (H_g) was calculated from the specific diameter-height equation by inserting D_g . Table 2.1 presents a summary of the data.

2.3 Data ranges

The stands in the data were all essentially even-aged and mono-specific and represented a wide range of initial spacings and thinning treatments, from

¹Experiments (year trees were positioned): A (1923); BL (1904); CB (1906); CN (1903); DA (1908); DB (1905); DE (1923); DF (1926); DI (1904); DL (1923); DM (1923); DO (1931); K (1908); M (1907); Q (1902); U (1908)

Table 2.1: Summary statistics of dominant height H_{100} , age (T), quadratic mean diameter (D_g), stem number (N) and basal area (G).

Variable	Unit	N	Mean	Minimum	Maximum	Std. Dev.
H_{100}	m	1600	21.22	5.08	36.95	7.74
T	years	2018	67.42	14	211	40.30
D_g	cm	2018	29.62	2.70	90.57	18.90
N		2018	1304.05	0.49	24720.45	2216.68
G	$m^2 ha^{-1}$	2018	20.22	0.21	73.58	9.23

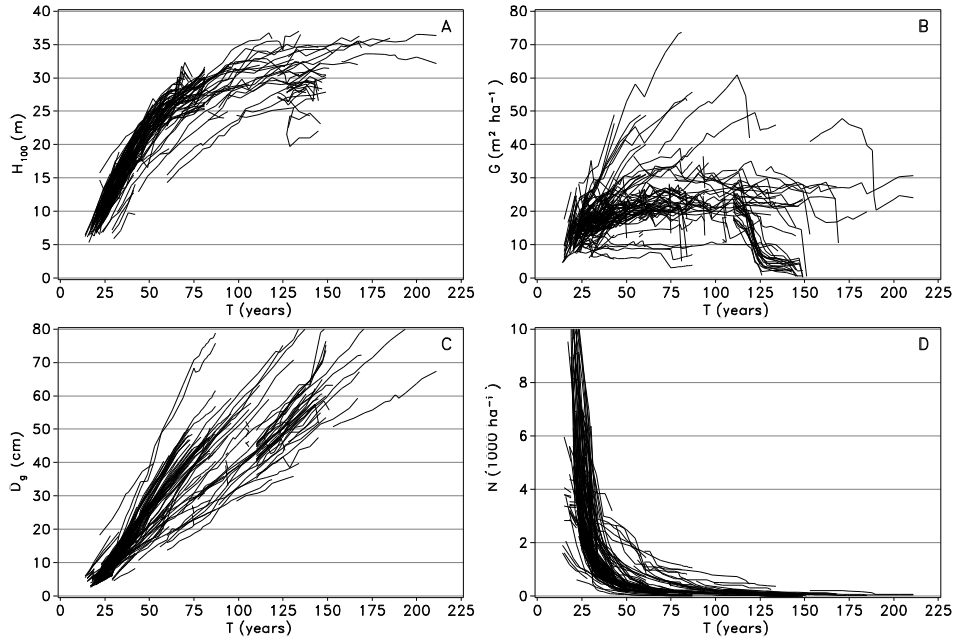


Figure 2.3: Stand-level values of H_{100} (A), G (B), D_g (C) and N (D).

unthinned controls to heavily thinned stands (Figure 2.3). In the thinning experiments, treatments ranged from unthinned controls to heavily thinned shelterwoods. In other experiments, plots were managed according to specific thinning strategies, such as group- or selection-thinning, and others were managed according to the thinning strategy typical at the time. However, plots were generally thinned from below with the objective to obtain a homogenous stand, which make the data less suited for modelling the growth of heterogeneous stands or stands thinned from above.

Stand ages ranged from 14 to 211 years, but the majority of measurement occasions were in stands from 20 to 100 years old (Figure 2.4). The number of measurements in very young (<20 years) and very old (>150 years) stands were relatively limited, which also limits the strength of derived models for applications at these extremes.

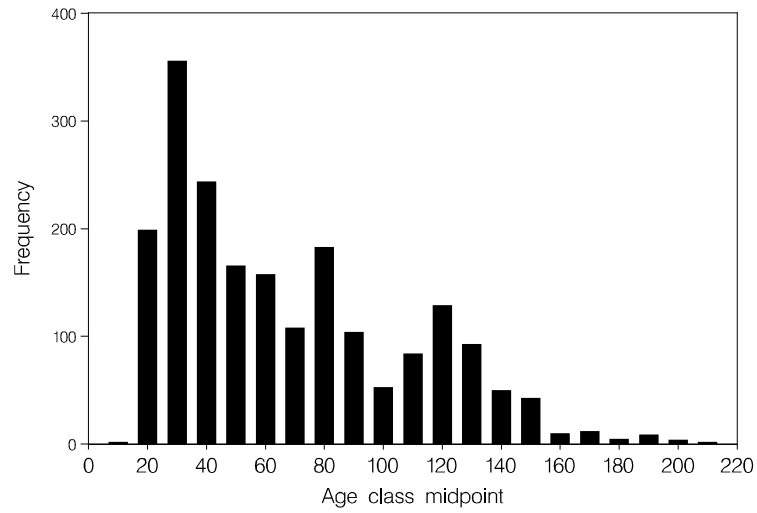


Figure 2.4: The number of measurements of stands in 20-year age classes.

Measured stands were mainly located on relatively good sites in the eastern parts of Denmark. Site-classes ranged from 11.8 to 28.3 m (height at age 50 years), but the majority of stands were in site-classes ranging from 20 to 24 m, which may be characterized as good beech sites (Figure 2.5). Consequently, the models derived from this data may not perform equally well on relatively low sites.

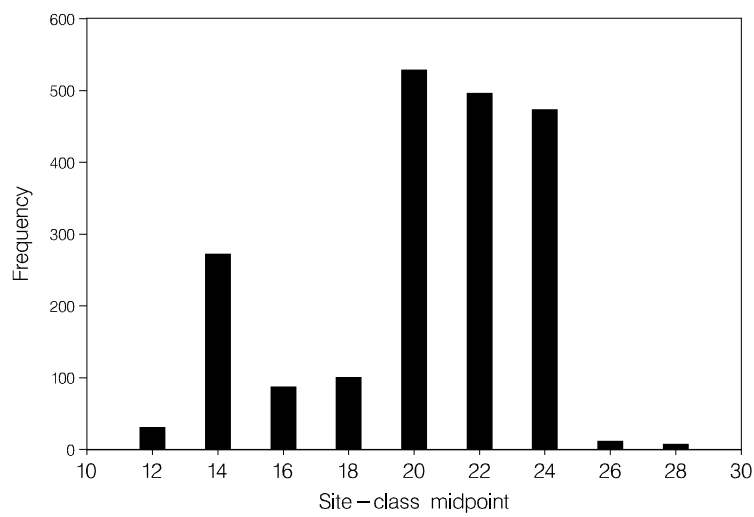


Figure 2.5: The number of measurements of stands in 20-year age classes.

Chapter 3

Modelling growth of beech in Denmark

Given the many applications of forest growth models no particular model is suited for all possible tasks. The present study focused on developing models describing beech growth at different levels of detail, suited for a wide range of applications. The work is presented in six individual manuscripts, of which five are submitted or accepted for publication in peer-reviewed, international forest research journals. The six manuscripts are found in the Papers-section of this dissertation and are:

- *Developing dynamic site index curves for European beech (*Fagus sylvatica* L.) in Denmark.* Accepted for publication in Forest Science.
(Paper I)
- *A state-space approach to stand growth modelling of European beech.* Submitted for publication in Forest Ecology and Management.
(Paper II)
- *A diameter distribution model for even-aged European beech in Denmark.* Submitted for publication in Forest Ecology and Management.
(Paper III)
- *Modelling individual-tree growth from data with highly irregular measurement intervals.* Accepted for publication in Forest Science.
(Paper IV)
- *Quantifying size-asymmetric growth among individual beech trees.* Accepted for publication in Canadian Journal of Forest Research.
(Paper V)
- *A spatially explicit individual-tree model.*
(Paper VI)

The last manuscript (Paper VI) presents the results from a preliminary study on spatial individual-tree models. This manuscript is not intended for publication in a scientific journal, but highlights some of the problems of spatial growth models and outlines the scope for future research in this area.

The following sections provide the background for developing models at different levels of resolution as well as an introduction to the individual manuscripts. Further, this introduction to the individual manuscripts aims at linking the individual growth models and providing perspectives for the application of the models as well as suggestions for future research within this field.

3.1 Assessment of site quality

The classification of agricultural lands into more or less productive ones is as old as agriculture itself. Such classification has been used for estimating the value of traded land, as basis for collecting taxes, or for predicting expected yields of agricultural crops. The classification of agricultural lands is usually based on the volume or weight of the crop produced, thus the measure of site quality varies between crops.

In many respects, the classification of forest lands is similar to the classification of other agricultural lands as the classification is based on the volume production of the primary product, namely wood. However, unlike other agricultural crops, the rotation of forest crops are many years and volumes are not easy to measure. Further, as forest stands are mostly thinned several times during the rotation, current volumes may tell little about the production capacity at a particular site as current volumes are influenced by the applied thinning regime and the time since last thinning. In practice, the forester may know little about the previous treatment when assessing site quality, hence although total volume production at some age may be the correct measure of site quality, it may have little practical value other than for research on permanent sample plots where all thinnings are known.

Due to the importance of a rational classification of forest sites and the difficulties in obtaining such a measure, the classification of forest soils has been a subject of great controversy. A scheme for evaluating site quality should:

- allow quick and relatively accurate determination of site quality in the field
- be universally applicable
- allow determination of site quality for all forest lands regardless of current state

- be flexible enough to allow comparisons across different regions while still being applicable locally

3.1.1 Determining site quality

Classifying forest sites by physical factors (e.g. elevation, topography, parent material, and climatic characteristics) is truly fundamental and is appealing because it provides a causal explanation for the observed production potential and offer insight into the ecological factors determining growth (Zon, 1913). Czarnowski (1964) developed an equation for predicting production capacity anywhere in the world based on four species properties, three climate parameters, and three soil parameters. Farr and Harris (1979) showed that growth of Sitka spruce was highly correlated with latitude and mean annual growing degree days. Studies on beech in Denmark have shown correlation of growth with soil properties and nutrient status (Holstener-Jørgensen, 1958; Callesen, 2003, pp. 117-139), while studies in Germany have modelled growth of mixed-species stands from combinations of several factors (Pretzsch et al., 2002). However, the production potential of a particular site is the result of complex interactions between multi-dimensional physical, ecological, and species specific factors and it remains a task of great difficulty to demonstrate and express environment-productivity relationships in suitable growth models.

A classification system based on the biotic characteristics of the forest has been suggested by a number of authors. The underlying assumption is that ground vegetation and wood production are influenced by the same environmental factors. Thus, according to this notion the vegetation reflects the complex sum of ecological, climatic, geographic interactions also affecting forest growth (Bornebusch, 1923; Daubenmire, 1976). In his classic study on forest types Cajander (1913, p. 164) found that the production potential is largely the same within individual forest types, determined by their floristic characteristics, and that production potential differs largely among different forest types. This led him to state that: *"Hereby it is in my view proven that forest types may be used as basis for the development of local yield tables"*. Similar findings are presented for Danish beech forests by Bornebusch (1923). Based on the observation that floristic characteristics may express production potential, such characteristics have been used as integrators of environmental factors to create indices of forest growth (Bornebusch, 1920, 1923; Rowe, 1956; Daubenmire, 1976). The use of climax forest type or floristic characteristics as basis for a classification scheme is however of little value when the forest or vegetation type cannot be observed e.g. when the specific species are not present on or in the vicinity of the forest area in question or when the climax forest type or floristic characteristics has not yet developed, for example as a consequence of recent forest fire or the silvicultural treatment. Further, such classification system is in-

herently subjective and remains a rather imprecise science (Vancley, 1994, p. 149).

Rather than determining site quality from causal factors a classification system may be based on observed growth of the current forest stand. As volume production is generally the parameter of interest, site quality may be evaluated directly in terms of observed volume production. Apart from the problems of identifying prior thinnings, such a scheme must be based on a reliable measure of volume. Merchantable or sawn volumes are generally unreliable as they depend on the trends in the market, vagary of fashion, and the conversion factor. Solid volume under or over bark thus provide a much more suitable measure of volume production as it is unaffected by various trends (Assmann, 1961, pp. 154-182). In 1888, the German Association of Forest Experiment Stations, classified forest sites by the current solid volume over bark per hectare of 100 years old stands of beech, pine and spruce/fir (c.f. Schwappach, 1893, p. 30). These tables did not allow for general comparisons of forest sites across Germany, as it was long before recognised that current volume was heavily influenced by the silvicultural practise. Instead it was recognised that the total volume produced was a far better measure of site quality (Schwappach, 1908).

Although total solid volume production provide a reliable measure of site quality it may have little scope for practical applications as discussed above. As early as 1877, von Baur (pp. 4-6) recognised that *site index*, the expected height at some base-age, may serve as a proxy for volume production. This was supported by later findings that stand volume was the same for a given mean stand height across site classes or in other words that stand volume is a function of mean stand height and is independent of stand age or site quality (Eichhorn, 1904). This was later referred to as the *Eichhorn rule of growth*. The Eichhorn rule of growth implies that volume production follows the same production-height path regardless of other stand factors and only the speed is affected by site quality ¹. This finding reduces the problem of determining site quality to a matter of defining the height-age pattern and obtaining a measure of height for the particular stand.

Classifying forest production by the height obtained at a specific age (site index) has been adopted by numerous authors everywhere in the world (e.g. Schwappach, 1911, pp. 141-142; Frothingham, 1921; Møller, 1933; Meyer, 1940). Although site index has been widely accepted as a measure of site quality, no concept of forest growth modelling has been more fiercely debated. A number of authors suggested including diameter growth, the second component of volume increment, when determining site quality (Parker,

¹The original formulation of the Eichorn rule of growth was: " ..., that a specific average stand height for all site classes corresponds to the same current volume, in other words that the current volume, independent of age and site quality, is a function of average height.". Only later was the rule formulated as the remarkably consistent relationship between stand height and *total* volume production.

1942; Stout and Shumway, 1982). However, although diameter growth is considered more sensitive to environmental factors, most modellers of forest growth have refrained from using this measure because of its dependence on the applied thinning regime.

Early Danish height curves for beech were produced by Gram (1879), who estimated mathematical functions for the development of normal yield tables. A series of height growth curves were subsequently developed for beech by various authors (e.g. Gyldenfeldt, 1881; Holm, 1892; Holten, 1894; Oppermann, 1914). Møller (1933) refuted the use of mathematical models in site curve modelling and developed a number of site curves and yield tables for beech based solely on graphical methods. These remain the most commonly used site curves in Danish forestry today. Later works for beech in northern central Europe include Carbonnier (1971), Schober (1972, pp. 4-41, A4-A47), Stuhr (1978), Henriksen and Bryndum (1996, pp. 82-107).

3.1.2 Estimating site index curves for European beech in Denmark

Apart from early attempts with graphical smoothing of the height-age relationship, most recent work on site index curves involves fitting of functions of the general form $H = f(t, S, \beta)$ where t is some age, S is the height at base age and β is a vector of parameters. These functions predict height as a function of age and site index. Such functions are often called static or base-age specific models because they predict height as a function of age and a site index at a fixed base-age obtained from a direct height measurement.

When fitting base-age specific site curves to repeated measurements on permanent sample plots, assessment of base-age and site index may be a problem because such data rarely have height measurements at an age common to all plots. Hence, heights at the desired base-age must be obtained from inter- or even extrapolations for all plots not measured at the chosen base-age. A different type of models unequivocally defines the individual site curves from any age-height point on the curve. Such base-age invariant models evade the need for prior assessment of site index as height at base-age is expressed explicitly by any height-age observation on the site curve. Hence, site curves may be estimated from permanent sample plot data without any inter- or extrapolations to obtain site index. In the paper *Developing dynamic site index curves for European beech (Fagus sylvatica L.) in Denmark* (Paper I), base-age invariant site index curves for European beech, are fitted to permanent sample plot data.

The base-age invariant model is fitted using the Generalized Algebraic Difference Approach (*GADA*) developed by Cieszewski (2001, 2003); Cieszewski and Bailey (2000). This approach involves four distinct steps:

1. Select the basic equation form. This step is often performed using

base-age specific methods to evaluate how well the different equations represents the data.

2. Identify the site-specific parameter in the basic equation. Although in their original formulation of the *ADA* (*Algebraic Difference Approach*) Bailey and Clutter (1974) describe models where site index depends solely on one parameter, any number may be specified in the *GADA*.
3. Generalize the site-specific parameters in the equation as functions of X , where X is an unknown measure of site quality. This step separates the *GADA* from *ADA* since introducing a function for the site-specific parameter allows it to vary across sites.
4. Solve for X and substitute for the independent variables, t and H , the initial conditions, t_0 and H_0 . The X in the equation developed in step 3 is finally replaced by this solution for X .

The methodology is first demonstrated on the flexible Chapman-Richards equation (Richards, 1959). Although suitable for demonstration purposes, this equation did not adequately describe the observed height growth pattern. Instead a *GADA* formulation of the logistic site equation by Monserud (1984) presented by Cieszewski (2001, Equation (21)) was used for modelling height growth:

$$H = H_0 \frac{t^{\beta_1}(t_0^{\beta_1}R + \beta_2)}{t_0^{\beta_1}(t^{\beta_1}R + \beta_2)} \quad (3.1)$$

where:

$$R = Z_0 + \left(Z_0^2 + \frac{2\beta_2 H_0}{t_0^{\beta_1}} \right)^{0.5}$$

$$Z_0 = H_0 - \beta_3$$

This equation is highly flexible and holds a number of desirable properties such as variable asymptotes and polymorphism. The model was fitted with a generalized least squares procedure, explicitly modelling the autocorrelation of observations from the same sample plot.

Based on the findings of this study, estimation of the base-age invariant form of the various equations used only tenable statistical assumptions and provided a significant improvement to the distribution of residuals. Further, the base-age invariant method evaded the need for prior information on site index and allowed for estimation without interpolation or extrapolation from the original data. The lack of a predetermined base-age implied that all of the data to be used in modelling the site equations regardless that the individual sample plots neither contained measurements at any base age

common for all the sample plots nor did share the same range of ages. For example compared to a base age of 50 years, this allowed for the utilization of twice the amount of observations of height and age from three times as many experiments.

3.1.3 Application of the site index curves

The site equation (3.1) may be applied for estimating dominant height at any age provided that dominant height is known at the current age. One practical application is to determine the site index for a given base-age and use this value in the stand and individual-tree level models presented in Paper II and IV, which both allow site index as a parameter determining site quality. We may consider a stand measured at age 42, having a dominant height of 15.1 m and wish to estimate the site index for a base-age of 100 years. Using equation (3.1) we find that:

$$Z_0 = 15.1 - 36.8647 = -21.5708$$

$$R = -21.5708 + \left(-21.5708^2 + \frac{2 \cdot 4087.59 \cdot 15.1}{42^{1.7184}} \right)^{0.5} = 4.2004$$

$$H_{T=100} = 15.1 \cdot \frac{100^{1.7184} \cdot (42^{1.7184} \cdot 4.2004 + 4087.59)}{42^{1.7184} \cdot (100^{1.7184} \cdot 4.2004 + 4087.59)} = 28.7m$$

Another application of the model is the prediction of height at a specific age given site index. Examples of such calculations are presented in Figure 3.1, where the site curves of the most commonly used yield table for beech in Denmark (Møller, 1933) are compared with the corresponding height curves of the site index equation (3.1). The comparison is made by substituting T_0 and H_0 in Equation (3.1) with the base-age 100 and corresponding height for the individual site classes and subsequently calculating heights for a range of values of T . The early height growth predicted by the site index equation is faster than predicted by the yield table for good sites but slower for poor sites. Further, height growth in old beech stands is more progressive than predicted by the yield table, especially for poor sites. The latter is consistent with a later revision of the yield table (Møller and Nielsen, 1953).

3.1.4 Estimation of the height of the mean basal area tree from dominant height

The comparison of the site index equation (3.1) and the site curves by Møller (1933) was carried out ignoring the fact that the site index equation was

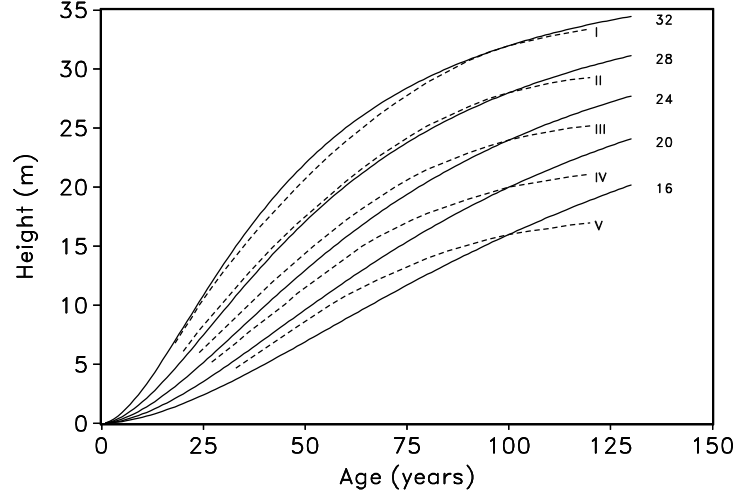


Figure 3.1: Comparison of the site index curves estimated from Equation (3.1) (full lines) with the site class curves from a Danish yield table for beech (Møller, 1933, dashed lines).

estimated for dominant height (H_{100}) whereas the yield table was based on the height of the mean basal area tree (H_g). This was done because the height growth patterns of the two measures of height are very similar. However, one may estimate H_g from H_{100} to correct for differences in the two measures of height.

Based on 1380 pair-wise observations of H_g and H_{100} , a graphical analysis showed that the relation between the two was close to linear (Figure 3.2) and a statistical analysis showed that a quadratic model fitted the data well. The model was fitted using a mixed effects model with a random effect for the individual plots:

$$H_{g,i,j} = \mu + \alpha(H_{100,i,j}) + \beta(H_{100,i,j}^2) + a_j + \varepsilon_{ij} \quad (3.2)$$

where $\varepsilon_{i,j} \sim N(0, \sigma_i^2)$ is the "white noise" of observation i at plot j , $a_j \sim N(0, \sigma_j^2)$ is the random plot effect, and μ , α , and β are parameters to be estimated.

Parameters of the model were all significant ($P \leq 0.05$, Table 3.1) and the model accounted for more than 99% of the variation ($R^2 = 0.991$). Residuals had zero mean but were not normally distributed. However, due to the amount of observations the deviation from normality probably has little influence on model inference. The distribution of the random plot-effect did not differ significantly from normality.

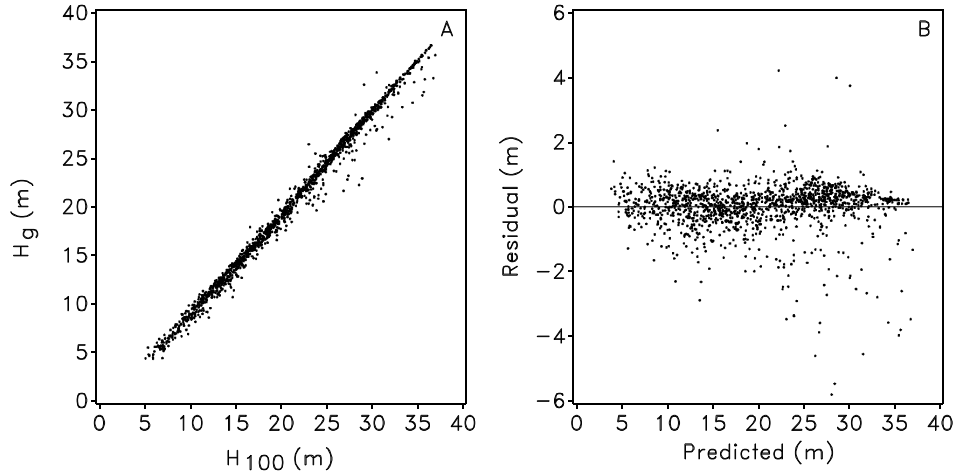


Figure 3.2: (A) The relation between dominant height (H_{100}) and the height of the mean basal area tree (H_g). (B) Residual plot of the relation between H_g and H_{100} fitted with a quadratic model (3.2).

Table 3.1: Parameter estimates of the quadratic relationship between H_g and H_{100} presented in Equation (3.2).

Parameter	Estimate	Std. Error	t value	$P \geq t $
μ	-1.0262	0.1372	-7.48	≤ 0.0001
α	0.9539	0.0131	72.73	≤ 0.0001
β	0.0022	0.0003	6.81	≤ 0.0001

3.2 Stand-level growth models

Stand-level growth models are models in which the basic units are stand-level variables such as basal area, stand volume, stem number, diameter of the mean basal area tree, dominant height etc. Such models represent simplistic representations of the forest stand but also generally require little information to predict forest growth. Thus, the general information produced by stand-level models are of great value to forest practice as necessary information can easily be obtained in the forest to make predictions of future yield, expected revenues, or expected demands for machine or man power.

The ease of obtaining information and making predictions using stand-level growth models have stimulated the development of numerous models for many different forest tree species around the world. Despite the vast amount of stand-level growth models available, the development of such models remains an area of active research.

Yield tables The simplest form of stand-level growth models are yield tables that represent expected yields from even-aged, monospecific stands tabulated by stand age and site class. Most yield tables include not only expected yields but also other stand-level variables such as stand height, basal area, stem numbers etc. The first yield tables were published in Germany in 1787 (c.f. Vuokila, 1966, p. 10). By 1880, 1,215 yield studies had been published for different species in Germany alone and since then thousands of yield tables have been developed for predicting forest growth across the world.

Generally speaking, the first German yield tables were based on graphical fitting of the stand factors against age of the stand. This approach requires some grouping of the research material into homogeneous classes of "poor", "mediocre", "good", or "excellent" growing conditions. In most studies, such site classification has been based on the age and the physical dimensions of the growing stock. In 1888 the German Federation of Forest Experiment Stations (*Verein Deutscher Forstlicher Versuchsanstalten*) decided to classify forest sites by the current volume at a specific age (c.f. Schwappach, 1893, p. 30). The choice of volume to classify forest sites is reasonable as volume production is usually the growth parameter of greatest interest (see also section 3.1.1, page 23). This quantity is however largely dependent on the thinning regime and difficult to assess, especially when stands are of different age. The problems of determining site from current volume is noted by Schwappach (1893, pp. 29-30), who also notes that although the average height is somewhat dependent on the thinning regime, dominant height is generally independent of stand density. Provided these considerations it is rather peculiar that Schwappach in this and in his later yield table for Scots pine (Schwappach, 1908) decided to use current volume at stand age 100 as the site class determinant. First in his yield table for beech, Schwappach (1911, pp. 93-168) used the average height at age 100 as determinant of site class. All later yield tables for beech are using some measure of height as the determinant of site class.

In 1877, von Baur, (pp. 16-40) developed the first yield tables that use stand height as a measure of site quality. The yield tables were developed from 99 experimental plots by first dividing the stands into equidistant age classes. The average stand height in each of the classes was divided into four equally wide classes and a graphically smoothened height curve was drawn through the mid-points of the age-height classes. Based on this system of age-height curves, the 99 experiment plots were divided into site classes and average basal area per ha 1.3 m above ground was calculated for each age and site class. For each site class a smooth age-basal area curve was drawn. A similar approach was used for deriving age-stem number and age-volume curves of the remaining stand. The individual curves were finally tabulated to provide a yield table for each site class. These yield tables could be used for site classification, estimation of stand factors at a given age, and for

assessment of the culmination of volume production but did not provide information on expected yields in thinnings.

Many of the yield tables developed in Germany and elsewhere were merely local tables, characterizing local growth conditions and thinning practises. However, yield tables for beech of a more general nature were presented for Germany by Schwappach (1893, 1911); Wiedemann (1932); Schober (1972); Stuhr (1978), for Sweden by Petrini (1938); Carbonnier (1971), for France by Pardé (1962), and for Switzerland by Badoux (1939).

Danish yield tables A thorough analysis and classification of Danish yield tables in the past century is provided by (Holten-Andersen, 1989).

The first Danish yield tables were developed by Reventlow in 1816 (c.f. Holten-Andersen, 1989). These "experience tables" represents the expected growth of "properly spaced" oak and beech trees on "good forest soils" for a 120 year rotation. Stand factors were derived by assuming that height growth was 1 foot per year the first 40 years, 2/3 of a foot the following 40 years and 1/3 of a foot the last 40 years. Annual diameter increment was assumed to be 1/4 of an inch during the entire rotation. Spacing of the remaining stand was determined by assuming a square spacing and by describing the height/diameter ratio as a function of age. Further, thinned stem numbers were based on an assumption of no self-thinning. Finally the remaining stand factors were derived by assuming that for the first 40 years the trees had the shape of a cone, but volume later "approaches more and more the volume of a cylinder half as long as the tree and with a basal area corresponding to the basal area at the butt" (Reventlow, 1879, pp. 193-196).

In the early Danish yield studies, the research material originating from temporary or permanent sample plots was plotted against stand age to identify trends of the material. Based on the observed trends, an analytical expression was sought and used for deriving stand factors. Hereby, early Danish scientists introduced the basic ideas of a functional approach to developing yield tables. This approach was first used by Gram (1879), who first expressed the height-age relationship as:

$$h_x = ax^n c^x \quad (3.3)$$

where h is stand height, x is stand age, and a , n , c are parameters to be estimated. Parameters were estimated for each site class by linearizing (3.3) by log-transformation and solving the equation using three observations of stand age and height. Subsequently, the diameter of the mean basal area tree (D_g) was estimated as a linear function of stand age. By using a fixed time interval between thinnings and assuming a constant relation between thinned numbers of stems in subsequent thinnings, Gram expressed the stem numbers between thinnings as:

$$s_{x+m} = a + bc^x \cdot c^m \quad (3.4)$$

where x is stand age, m is thinning interval and a , b , and c are parameters to be estimated.

Gram (1879) did not proceed to develop normal yield tables, but only presented his findings in three curves, that represent the current stand at the midpoint between thinnings. However, the ideas presented in this work inspired the development of a series of yield tables based on the functional approach (Gyldenfeldt, 1883; Gram, 1889; Oppermann, 1914).

The derivation of mathematical expressions of stand factors demonstrated by Gram (1879) was very advanced for its time and represented a significant leap forward. These methods are objective, easy to reproduce and allow for making biological as well as mathematical inference of the processes governing tree growth. Nevertheless, the work presented by Møller (1929, 1933, and later works) abandoned the mathematical smoothing of stand factors, using the faster and cheaper graphical method. After 1930, practically all yield tables until 1980 were based on subjective graphical smoothing of the stand factors rather than on objective statistical methods. First in 1983, Magnussen developed yield tables for Norway spruce based on rigorous statistical analyses of the variation of stand factors. Even in the latest yield table for beech in Denmark (Henriksen and Bryndum, 1996, pp. 82-107), such tools were only applied after the development of the yield tables for constructing a mathematical representation of the tables (Wunch, 1996).

Growth equations Conceptually, yield tables and stand-level growth equations are very similar as mathematical growth equations can easily be expressed in a tabular form. This is in fact the case in the yield tables for beech by Gyldenfeldt (1883), Gram (1889), and Oppermann (1914). However, the opposite is not possible and in contrast to the yield tables, growth equations are a convenient way to express growth and yield on present day computers. Further, the methodologies involved in developing such growth equations are objective, easy to reproduce, and allow for rigorous statistical testing of assumptions.

During the 1930's a significant generalization of the procedure for developing growth equations was achieved. In 1939, MacKinney and Chaiken were presumably the first to develop empirical yield tables based on statistical techniques in place of the earlier graphical methods and the methods applied by Gram (1879) and others. They used multiple linear regression techniques to predict the logarithm of yield as a function of stand variables (age, site, density, and composition). With certain modifications, their approach has been employed in most recent models of forest growth (Clutter, 1963).

Following the advances of MacKinney and Chaiken (1939) a large number of growth equations based on statistical approaches have been developed for different stand factors (e.g. Meyer, 1940; Petterson, 1955; Franz, 1971). In a number of these studies, growth and yield are modelled as independent phenomena, despite the logical compatibility between increment and aggregated volume (Bertalanffy, 1949). In his work Clutter (1963) explicitly expressed the relationships between growth and yield, when developing compatible growth and yield models for loblolly pine, and proposed a system of related equations for volume and basal area growth. If the variables of such a system of equations are interdependent, the system of equations may be referred to as *simultaneous*. If the system of equations can be ordered such that each dependent variable is expressed as a function of the independent variables and only those dependent variables which were subject of the previous regressions, the system is said to be *recursive*. Finally, if the only relation between the individual equations is error correlations, the system is said to be *seemingly unrelated*. If no error correlation exists, the individual regressions may be treated as individual estimation problems. However, if functional interdependencies or statistical correlations are ignored, ordinary least squares lead to biased, inconsistent or inefficient estimates of regression coefficients. Methods that implicitly recognize functional relationships and error correlations have been applied to forest and yield models amongst others by Sullivan and Clutter (1972); Ek (1974); Ferguson and Leach (1978); Borders and Bailey (1986); Borders (1989).

3.2.1 A dynamic stand-level growth model for beech

Static models of forest growth, such as yield tables or closed-form mathematical models, fail to recognise that forest stands are dynamic systems, subject to sudden changes caused by e.g. silvicultural interventions. When the actual thinning practise differs from that of the equation or table, the model can no longer be expected to yield sensible predictions of forest growth and yield. Changing price structures, varying goals of forest owners, and various calamities during the lifespan of the stand frequently alter the applied silvicultural practise. Therefore, the importance of developing dynamic models for forest management planning is evident.

The development of dynamic growth models constitutes a shift from purely empirical models towards deductive and causal models. Purely empirical models, such as yield tables, describe stand development as a function of time given the applied thinning regime. If the thinning regime is changed, reasonable predictions can only be obtained by changing the entire model. An adequate causal model on the other hand allows modelling of any shifts in silvicultural practise during the lifetime of the stand without changing the model as the underlying processes of growth remain unchanged and are captured by the model.

Truly causal models for predicting forest growth are difficult to obtain as the underlying processes and interactions governing tree growth are not very well understood. Further, the application of such models would probably be impossible because of the level of information required for such a model. A promising compromise is provided by the "state-space" approach (García, 1994). The hypothesis underlying this approach is that the current state of the system characterizes the past causes of the system and constitutes all the information needed to predict its future behaviour. For instance, using this approach an even-aged beech stand may be characterized by the current basal area and dominant height and predictions of future basal area growth does not depend on the timing and intensity of thinnings leading to the current state of the system.

In the state-space model it is assumed that the n dimensional state vector at some point in time, $\mathbf{x}(t)$, can be predicted by the transition function \mathbf{F} of the state variable, $\mathbf{x}(t_0)$, and a vector of input variables, \mathbf{U} at some other point in time (after García, 1994):

$$\begin{aligned} \mathbf{y}(t) &= \mathbf{g}[\mathbf{x}(t)] \\ \mathbf{x}(t) &= \mathbf{F}[\mathbf{x}(t_0), \mathbf{U}, t - t_0] \end{aligned} \quad (3.5)$$

where the current output, \mathbf{y}_t is a function \mathbf{g} of the current state. In other words the state-space approach predicts any future states of the system from the initial state, $\mathbf{x}(t_0)$, through iteration. For example an initial observation of the two-dimensional state vector of height and basal area may be used to predict basal area and height after one period. The new estimates of the two state variables are then re-entered into the model to predict the state after one more period and so forth. Abrupt changes in e.g. basal area due to thinnings are handled by simulating the shifts in the state vectors and are seen as shifts between different growth paths (Figure 3.3).

In the paper *A state-space approach to stand growth modelling of European beech* (Paper II), a dynamic stand-level model for beech is developed using the state-space approach. The model is based on permanent sample plot data, covering a wide range of initial spacing and thinning practises. The model entails three equations for predicting dominant height growth (ΔH_{100}), basal area growth (ΔG), and mortality (ΔN):

$$\begin{aligned} \frac{\Delta H_{100}}{\Delta t} &= \alpha_1 H_{100}^{\alpha_2} e^{\alpha_3 H_{100} + \alpha_4 G} \\ \frac{\Delta G}{\Delta t} &= (\alpha_1 \cdot \beta_{02}) G^{\beta_2} e^{\beta_3 G + \beta_4 H_{100}^{\beta_5}} + FV[G] \\ \frac{\Delta N}{\Delta t} &= \gamma_1 N^{\gamma_2} e^{\gamma_3 \sqrt{N} H_{100}} + FV[N] \end{aligned} \quad (3.6)$$

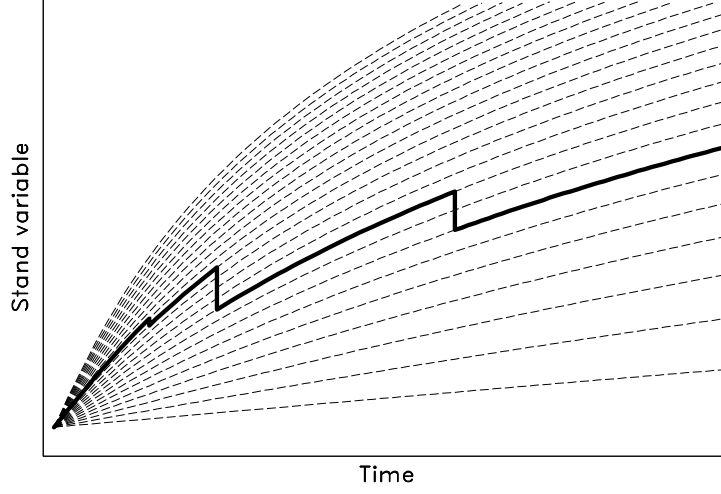


Figure 3.3: Illustration of a dynamic stand-level model. Silvicultural interventions are merely shifts from one growth path to another.

where α_1 is a site-specific parameter estimated locally and $\alpha_2 - \alpha_4$, β_{02} , $\beta_2 - \beta_5$, and $\gamma_1 - \gamma_3$ are parameters estimated globally. $FV[G]$ and $FV[N]$ are forced shifts in basal area and stem numbers caused by thinnings.

A special problem related to the estimation of dynamic models is that of determining periodic increment when measurement intervals differ from the desired interval of the model. The simplest way to deal with discrepancies between actual and desired measurement intervals is to assume that periodic increment is constant between measurements and equals the average growth rate. In that case periodic growth rate may be estimated by a linear interpolation between measurements. However, in case of a concave increment trajectory, such interpolation leads to underestimation of periodic growth, whereas the opposite is true when the increment trajectory is convex (Figure 3.4A, B; McDill and Amateis, 1993).

In this study, measurement intervals varied from 1-28 years, implying that procedures was needed which avoided arbitrary assumptions about the unobserved periodic growth. Using the state-space approach, a seemingly unrelated estimation procedure was used to estimate the parameters θ , of each of the equations in (3.6) by:

$$\min \sum_{j=1}^n (x_m - \mu)^2 \quad (3.7)$$

$$x_m = F(t_i - t_{i-1}, x_{i-1}, \theta) + \epsilon_i, i = 1, 2, \dots, m \quad (3.8)$$

In words, the growth from each observed starting value was iterated to

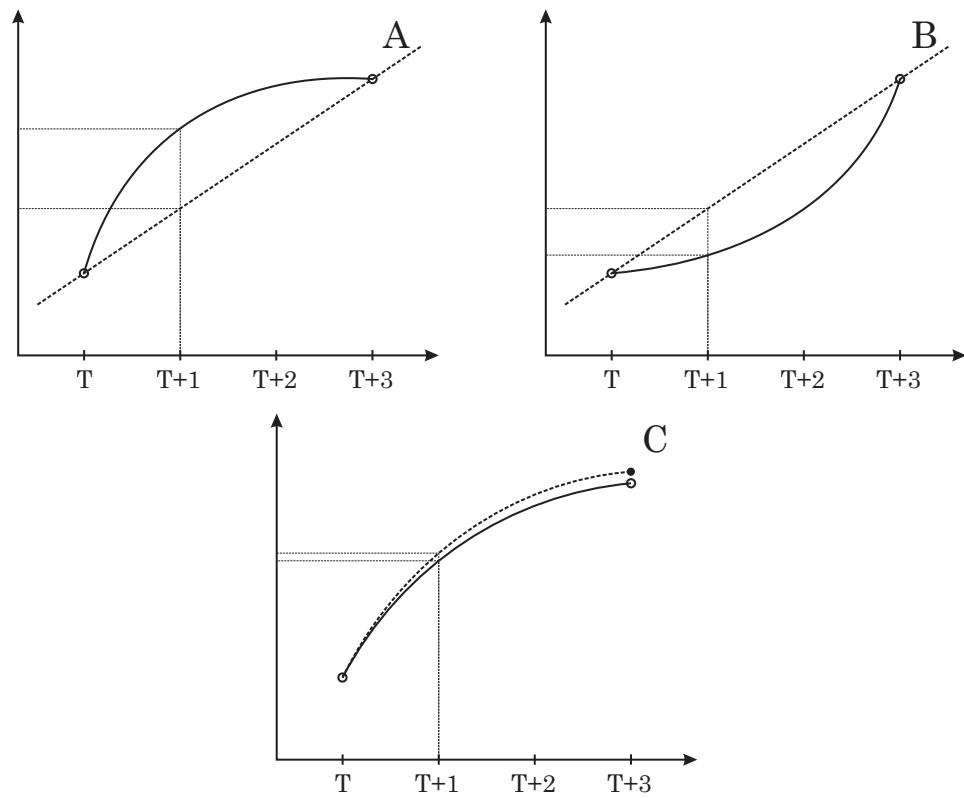


Figure 3.4: Biased estimates of annual increment caused by linear interpolation when the growth curve is A) concave and B) convex (based on McDill and Amateis, 1993, Figures 1a, 1b, and 2). C) represents an interpolation method that uses the proposed growth model for interpolation.

the corresponding value of the following observation, using the years between individual measurements as the number of iterations. Hereby, the estimated equation itself was used to predict unobserved interim values of the state variable, presumably providing a better interpolation than those obtained when assuming linear growth between measurements (Figure 3.4 C).

The model in Equation (3.6) uses one site-specific rate constant (α_1) as indicator of site quality. This indicator is estimated from both height and basal area growth, thereby combining the two factors of volume production. The model is dynamic in the sense that it allows continuous updates of the state variables when combined with records of thinning activities. Further, the rate constant may be continuously updated as more data become available. α_1 was highly correlated with site index, but showed no correlation with soil texture variables (fractions of clay, silt, sand, or coarse sand). Hence, to allow multiple sources of input, the model parameters were also estimated using site index as an indicator of site quality.

The stand-level growth model generally confirmed the anticipated growth paths of dominant height and basal area. Statistical tests indicated significant systematic deviations between observed and predicted values, but deviations were small and of little practical importance. An extensive cross-validation procedure was applied to evaluate the extrapolation properties of the model. These procedures indicated that the model may be applied across a wide range of growth conditions and thinning practices in Denmark without significant loss of accuracy.

3.2.2 Application of the dynamic stand-level growth model

The stand-level model can easily be applied in simulations to investigate alternative thinning regimes and to develop local yield tables for a specific thinning regime. A local yield table may be developed by initially selecting a set of starting values of stem number, basal area, and dominant height either from local experience or standard yield tables. These variables are identical to the vector of state variables $\mathbf{x}(t_0)$, \mathbf{U} in Equation (3.5). Further, thinning intervals, the applied thinning regime, and the thinning quotient Q (ratio of the stand diameter in the thinning and before thinning), are determined from local practise. α_1 is estimated based on consecutive observations of the state variables or the estimated site index.

Now, the yield table may be developed by following a series of steps outlined below and in the factor structure diagram presented in Figure 3.5:

1. State variables are iterated from the starting values using the number of years between thinnings as the number of iterations. Dominant height, basal area, and stem-numbers so obtained correspond to the state before thinning.

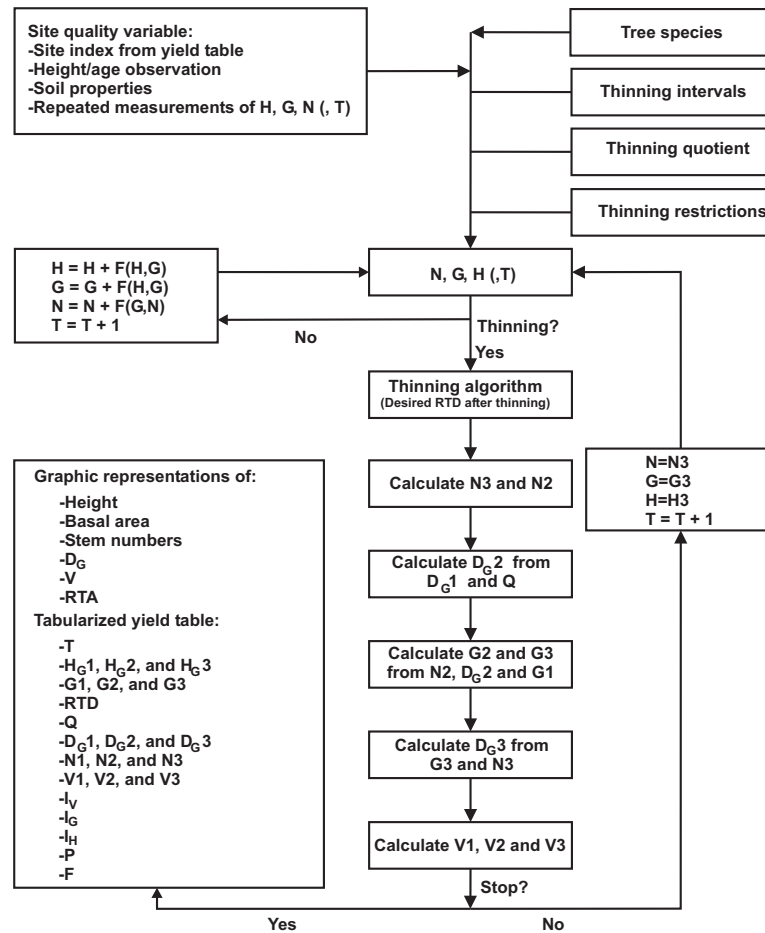


Figure 3.5: The structure of developing local yield tables, using the dynamic stand level growth model presented in Paper II. Numbers refer to the individual variables before (1) and after (3) thinning as well as for the thinned volume (2).

2. Thinnings are simulated by first assuming that dominant height is unaffected by the thinning, and stem number after thinning is then calculated from the height and desired relative spacing after thinning as $N = 10,000 / (RS \cdot H_{100})^2$.
3. Thinned number of stems is calculated as the difference between stem numbers before and after thinning.
4. Diameter corresponding to the mean basal area tree, D_g , in the thinning can now be calculated from D_g of the crop before thinning and the thinning quotient ($D_g(\text{thinning}) = Q \cdot D_g(\text{before thinning})$).
5. Thinned basal area is calculated from the thinned number of stems and D_g in the thinning ($G = N \frac{\pi}{4} D_g^2$).
6. Basal area after thinning is calculated as the difference between basal area before thinning and the thinned basal area.
7. Volume after thinning and the thinned volume can be calculated from any volume function for beech (e.g. Madsen, 1987).
8. The calculated state variables after thinning are now fed into the state-space model and the state variables are predicted until the next thinning through iteration.

As an example, two local yield tables were developed for beech with a site index of 20 m (base-age 50 years, see Appendix A). The stands were thinned every 5 years to a relative spacing (RS) of 0.14 for B-grade thinning and 0.18 for a C-grade thinning, corresponding to the values provided by Henriksen (1988, p. 323). The yield tables start at age 25 with 5,000 stems per hectare, basal area of $16 \text{ m}^2 \text{ha}^{-1}$, and a dominant height of 9.1 m.

It should be noted that when making yield tables, the model is very sensitive to the choice of starting values as state variables are often iterated over more than 100 years. Further, it should be noted that the models are weakly founded for poor sites ($H_{100} < 14$ m at age 50), for very good sites ($H_{100} > 24$ m at age 50) and for very young (<20 years) and very old (>150 years) stands. When the model is applied in very young stands (with low values of G and H_{100}), growth is generally underestimated (in fact, when G and H_{100} are zero, growth is zero as a consequence of the model formulation). In old stands, basal area growth is often observed to be somewhat overestimated especially when those stands are subjected to heavy thinnings.

3.3 Size-distribution models

Stand-level models are valuable tools for forest managers and researchers and provide fast and cheap information on growth and yield. However,

estimates of stand-level variables, such as stand basal area or mean diameter, are crude simplifications that do not include the considerable size variation often observed in actual forest stands. Size-distribution models predict the size distribution in forest stands from a set of stand-level variables and hence provide more detailed information without increasing the cost of obtaining the information needed to estimate the model parameters.

Many probability functions have been used to describe size distributions in forest stands, for example the negative exponential function (Meyer, 1933), the Gram-Charlier (Prodan, 1953), Beta (Clutter and Bennett, 1965), Gamma (Nelson, 1964), Weibull (Bailey and Dell, 1973), and Johnson S_B (Hafley and Schreuder, 1977) distributions. The utility of a specific probability function depends on its ability to reflect the observed size-distribution adequately. A common observation is that forest stands often become bi- or multi-modal because of the development of an understorey or due to a specific thinning regime. The above-mentioned models are all uni-modal except for the S_B distribution that can represent some bi-modal distributions. A possible solution is to use a finite mixture of distribution functions (Titterton et al., 1985; Zhang et al., 2001). A number of studies have further focused on the estimation of bivariate distributions of e.g. diameter and height to better characterize stand structures (Schreuder and Hafley, 1977; Hafley and Buford, 1985).

Size-distribution models may be estimated in various ways that fall into two categories. In the *parameter prediction approach* the model forecasts the future number of stems and the parameters of the chosen probability density function (pdf) characterizing the size-distribution of those trees. Stand variables such as basal area or diameter of the mean basal area tree may subsequently be derived by integration or summation. In the *parameter recovery approach* parameters of the diameter distribution function are estimated from particular stand-level variables such as basal area or dominant height. Parameter recovery is generally considered to give better results than parameter prediction (Reynolds et al., 1988).

The parameter recovery approach includes the following steps:

1. Select a desirable distribution function
2. Estimate parameters of the probability density function
3. Relate parameters to stand-level variables

Parameters of the desired distribution may be estimated in a variety of ways, depending on the available computational resources and the desired efficiency. Burk and Newberry (1984) used the first three non-central moments of the Weibull-distribution and an iterative procedure for moment-based recovery of the parameters of the pdf. (Borders and Patterson, 1990) used a

set of linear regressions to predict the 0th, 25th, 50th, and 95th percentiles for recovering the parameters of the Weibull-distribution. Among the different methods, maximum likelihood estimation (MLE) has been found to produce consistently better results. Cao (2004b) used MLE to estimate the scale (b) and shape (c) parameters of the Weibull-distribution, using an *a priori* estimate of the location parameter (a). An iterative procedure was used to search for parameters maximizing the weighted log-likelihood:

$$\sum_{i=1}^p \frac{1}{n_i} \ln(L_i) \quad (3.9)$$

where p is the number of plot-age combinations, n_i is the number of trees of the i th plot-age combination, and:

$$\ln(L_i) = \sum_{j=1}^{n_i} \left(\ln(c) - \ln(b) + (c-1) \ln \left(\frac{x_{ij} - a}{b} \right) - \left(\frac{x_{ij} - a}{b} \right)^c \right) \quad (3.10)$$

where x_{ij} is the diameter of the j th tree.

The parameters (b) and (c) were defined as functions of stand-level variables, and thus the MLE procedure estimated the parameters of those functions simultaneously. The weighing of observations by $1/n_i$ implies that equal weight is given to each plot-age observation.

Although MLE is often considered the superior method of estimating parameters of distribution functions it also put large demands on the computational capacity. Therefore, in a recent application Cao (2004b) identified parameters of the Weibull-distribution by nonlinear least squares estimation of the cumulative density function (cdf), minimizing the following function:

$$\sum_i^p \sum_{j=1}^{n_i} \frac{1}{n_i} \left(F_{ij} - \hat{F}_{ij} \right)^2 \quad (3.11)$$

where F_{ij} is the observed cumulative density of tree j on the i th plot-age combination, and \hat{F}_{ij} is the cdf of the chosen distribution. As with MLE estimation, parameters of the cdf were expressed as functions of stand variables, which allowed simultaneous estimation by minimizing the squared deviations between observed and predicted cumulative densities. Cao (2004b) found that among the various methods for estimating parameters of size-distribution models, MLE and CDF-regression were superior to moment- or percentile-based recovery of parameters.

3.3.1 A diameter-distribution model for beech

In the manuscript *A diameter distribution model for even-aged European beech in Denmark* presented in Paper III a diameter distribution model for

even-aged stands of European beech in Denmark was estimated using the Weibull-distribution.

Parameters of the model were estimated by fitting the cumulative density function by a non-linear least squares procedure, where the location (a), scale (b), and shape (c) parameters were formulated as functions of stand-level variables:

$$F(d_{ij}) = 1 - \exp\left(-\left(\frac{d_{ij} - a_j}{b_j}\right)^{c_j}\right), \quad (3.12)$$

$$a_j = D_{g,j} \left(1 - \exp(-a_1 D_{g,j})\right)^{a_2} + \varepsilon_{a,j}, \quad (3.13)$$

$$a_1 = a_{01} D_{g,j} H_{100,j}$$

$$a_2 = a_{02} + a_{03} \ln(N_j)$$

$$b_j = \frac{b_{01} D_{g,j}}{b_{02} + D_{g,j}} + \varepsilon_{b,j}, \quad (3.14)$$

$$c_j = \frac{c_1}{1 + c_2 \exp(-c_3 D_{g,j})} + \varepsilon_{c,j}, \quad (3.15)$$

$$c_1 = c_{01} + c_{02} N_j D_{g,j}^2$$

$$c_2 = c_{03}$$

$$c_3 = c_{04} \frac{D_{g,j}}{H_{100,j}}$$

where $F(d_{ij})$ is the cumulative probability of the Weibull-distribution evaluated at the diameter d_{ij} for the plot (i) and age (j) combination. The parameters of the distribution function are expressed as functions of dominant height (H_{100}), stem number (N), and the diameter corresponding to the mean basal area tree (D_g).

In addition to the un-constrained model, the parameters of Equation (3.15) were estimated, where the scale parameter (b) was constrained to yield estimates of the diameter distribution function, consistent with observed or predicted basal area:

$$b = \frac{-a\Gamma_1 + \sqrt{a^2 (\Gamma_1^2 - \Gamma_2) + \Gamma_2 D_g^2}}{\Gamma_2} \quad (3.16)$$

where $\Gamma_1 = \Gamma(1 + 1/c)$, $\Gamma_2 = \Gamma(1 + 2/c)$, and $\Gamma(\cdot)$ is the complete Gamma-function.

Estimated diameter distributions were evaluated by statistical tests that included t-tests of predicted mean and χ^2 , Kolmogorov-Smirnoff (KS) and Anderson-Darling (AD) goodness-of-fit tests.

Parameters of the diameter distribution model were successfully fitted using the CDF-regression and predicted distributions were in agreement with the expected development of diameter distributions in even-aged beech stands. Fit statistics were only slightly affected when the model was constrained to yield estimates consistent with observed basal area.

In 30-45% of the plot/age combinations, the estimated diameter distribution differed from the observed distribution according to the chosen evaluation criteria. The majority of the rejected distributions were irregular and would not be fitted successfully by any smooth statistical function. This irregularity is probably caused by thinning of specific types of trees and explains why stand table projection methods are generally more successful when predicting future diameter distributions. In a number of cases where the predicted distribution differed from the observed, visual inspection showed that the observed distribution was bi-modal due to the formation of understorey. Such distributions could be fitted by a finite mixture distribution model. However, as the understorey trees were treated very differently across the plots and at the same time had little influence on stand variables, the diameter distribution model cannot be expected to adequately model the distribution of understorey trees based on stand-level variables.

The frequency of failed distributions were considerably higher in young stands (<40 years) where 60-80% of the distributions differed from the predicted. The disappointing result for stands younger than 40 years is probably due to large differences in initial stem-numbers within the dataset. Hence, the diameter distribution model may be used for predicting distributions from observed or predicted stand-level values of stem numbers and basal area but care should be taken when the model is applied to young stands.

3.3.2 Application of the diameter-distribution model

The diameter distribution model may be used for predicting the development of stand structure of even-aged beech stands in Denmark, hereby providing an extra layer of information to existing yield tables or to growth and yield predicted using the stand-level model provided in Paper II. The information obtained may improve assessment of thinning costs and revenues as procurement costs and prices are strongly correlated with tree size. Further, the estimated diameter distribution may be used for simulating the assortment distribution, using an appropriate stem-taper equation.

The fraction of stems in any particular diameter class with class midpoint d_m and width $2w$ is calculated as:

$$n_i = \left[\exp \left(- \left(\frac{d_m - w - a}{b} \right)^c \right) - \exp \left(- \left(\frac{d_m + w - a}{b} \right)^c \right) \right] \quad (3.17)$$

where parameters a , b , and c are estimated from observed or predicted stand-

level values.

The fractions should (at least approximately) sum to 1. Stem numbers in the individual diameter classes are calculated by multiplying with total stem number and subsequent rounding to the nearest integer. The stem number of the estimated distribution may differ from the total stem number, and some minor corrections may be necessary.

Mean height of the individual diameter classes may subsequently be estimated from a suitable diameter-height model and, finally, the volume of each class may be calculated from a suitable volume equation (e.g. Madsen, 1987). Application of the diameter-distribution model is not expected to improve estimates of total volume compared to the mean tree method as the mean tree method is fairly accurate (from -3.4% to + 3.8%, depending on thinning intensity; Bryndum, 1980). However, the model may significantly improve assessment of the assortment distribution and hence the economic yield.

3.4 Individual tree growth models

The information provided by stand-level models is valuable to forest managers because the models require limited input data and the output is sufficiently detailed for management purposes. However, the aggregated information provided by the stand-level models is not sufficient for e.g. detailed investigations of the effect of silvicultural alternatives on stand structures or for analyzing specific thinning strategies such as target diameter harvesting vs. thinning from below.

The shortcomings of stand-level growth models have become increasingly evident in relation to the ongoing conversion towards near-natural forestry in Denmark. The aggregation made by using for instance a yield table for planning or research purposes may be valid in monospecific, even-aged management because the even-aged monocultures are relatively homogeneous. However, as the stands become increasingly diverse, existing growth models no longer provide a sufficiently detailed output to adequately describe the forest stands. It is for example of little interest to know that the mean diameter of a stand is 22.8 cm if individual trees diameters range from 0 to 112 cm. Further, the economic, biological or recreational consequences of converting to near-natural management are not known and can only be assessed through simulation because the conversion will probably take several hundred years. Hence, a need exists for the development of models that predict forest growth at the individual-tree level.

When modelling individual-tree growth, we may distinguish between spatial models, that simulate individual-tree growth using the spatial position of the trees, and non-spatial models which do not require spatial data. Whereas

the spatial models may provide valuable insight into the competitive interactions between individual trees they are limited by the fact that the measurements required for such models are expensive to obtain and seldom available for making yield predictions. Further, non-spatial models are often found to predict individual-tree growth just as good as or even better than spatial models (e.g. Biging and Dobbertin, 1992).

In the non-spatial model all trees in the plot influence each other in the same way irrespective of the distances between the trees. Such a model is obviously not a full description of the competitive relationships as neighbouring individuals will affect growth relatively more than more distant ones. Nevertheless, in many cases non-spatial models have been shown to model plant growth adequately and a mean field model is often a reasonable place to start in the modelling of plant-plant interactions (Bolker et al., 1997). Non-spatial models have amongst others been used to predict basal area increment and mortality of Austrian forest tree species (Monserud and Sterba, 1996, 1999), diameter increment and mortality of *Eucalyptus* sp. in Tasmania (West, 1981), Douglas-fir in Oregon (Bravo et al., 2001), and loblolly pine in Southern United States (Cao, 2000), and mortality, diameter, and height growth of various species in Oregon (Hann and Hanus, 2002a,b; Hann et al., 2003) and for Norway spruce in Denmark (Johannsen, 1999).

The effect of the spatial arrangement of the individual trees on tree growth was recognized by the Danish forester C.D.F. Reventlow in 1816 (c.f. Holten-Andersen, 1989). The influence exerted on the individual tree by other trees in its vicinity was also studied by Vuokila (1966), who found significant effects of the average distance to neighbouring trees and Lemmon and Schumacher (1962b) and Spurr (1962), who found an effect of point density of overstorey trees on periodic volume and diameter increment.

Most efforts on modelling the complex competitive interactions among individual trees aggregated the competitive effects into a competition index (e.g. Bella, 1971). Studies of spatial competition indices generally found that inclusion of spatial information provided little improvement to model efficiency (e.g. Opie, 1962; Lorimer, 1983; Tomé and Burkhart, 1989; Biging and Dobbertin, 1992; Pukkala, 1989). In a study of the predictive performance of various competition indices using annual data, yearly fluctuations of water availability was found to affect competition symmetry (Wichmann, 2001). This finding led Wichmann (2002, pp. 21-30) to hypothesize that annual variations in the mode of competition and, hence, in predictive performance of any competition index may explain why no particular competition index has been found to be best. Another explanation may be that strong microsite variations mask the influences of competition (microsite variation will produce positive spatial correlations whereas competition produces negative correlations), leading to the counter-intuitive conclusion that the spatial arrangement of trees has no effect on tree growth (Fox et al., 2001).

The spatio-temporal effects of forest growth and competition may be

dealt with by modelling the effects as unquantified random effects in a stochastic model (Stage and Wykoff, 1993; Fox et al., 2001). Another approach is to explicitly model the effects of temporal variation in process-based models. Most process-based growth and yield models used photosynthesis as the basic growth process underlying carbon assimilation (Bartelink, 2000; Brunner and Nigh, 2000; Mäkelä et al., 2000). However, a number of modelling efforts recognised the importance of other physiological processes such as nutrient and water balance for the control of photosynthesis (Linder, 2000). Process-based models have become increasingly important in the light of a possible significant climate change, as such models allow explicit modelling of the effects on forest growth (Korol et al., 1996). However, such models are seldom used as practical tools in forest management because 1) input variables such as precipitation or temperature are not known for the coming growing seasons which precludes efficient modelling of those effects, 2) process-based models often require a very detailed level of information seldom available to forest practitioners, and 3) the processes underlying tree growth are often not well understood and hence such models are usually less reliable than simple empirical models. An example of a process-based model for forest management is provided by Sands et al. (2000).

3.4.1 A non-spatial individual-tree growth model

Three individual papers on individual-tree growth models are included in this thesis, treating different aspects of individual-tree modelling. In the article *Modelling individual-tree growth from data with highly irregular measurement intervals* (Paper IV) a non-spatial individual-tree growth model was developed based on all the individual-tree measurements from the permanent sample plots (see Chapter 2). The dataset included a total of 276,000 diameter and 34,000 height measurements.

The model consists of three individual equations for predicting annual diameter and height increment and mortality. The underlying model form of the two growth equations is that of Zeide (1993) whereas the mortality model is based on a logistic model (Verhulst, 1845, 1847; cf. Skovsgaard, 1988):

$$\begin{aligned} \frac{\Delta d_i}{\Delta t} = & \exp\left(a_0 + a_1 \cdot \ln(d_{i,t} + k_1) + a_2 \cdot d_{i,t} + \right. \\ & \left. + a_3 \cdot G_t + a_4 \cdot \frac{G_{L,i,t}}{\ln(d_{i,t} + k_2)}\right) + \varepsilon_{d,i,t} \end{aligned} \quad (3.18)$$

$$\begin{aligned} \frac{\Delta h_i}{\Delta t} = & \exp\left(b_0 + b_1 \cdot \ln(h_{i,t}) + b_2 \cdot h_{i,t} + \right. \\ & \left. b_3 \cdot \frac{d_{i,t}}{h_{i,t}} + b_4 \cdot G_t + b_5 \cdot \frac{G_{L,i,t}^2}{\ln(d_{i,t})}\right) + \varepsilon_{h,i,t} \end{aligned} \quad (3.19)$$

$$P_{i,t} = \left(1 + e^{(c_0 + c_1 \cdot d_{i,t}^{-1} + c_2 \cdot G_{L,i,t})}\right)^{-1} \quad (3.20)$$

where $d_{i,t}$ is diameter at breast height (mm) and $h_{i,t}$ is total tree height (dm) of the i th tree at time t . Δd_i is diameter increment (mm) and Δh_i is height increment (dm) within a one-year growth interval (Δt). $P_{i,t}$ is mortality probability, G is basal area ($\text{m}^2 \text{ ha}^{-1}$), G_L is basal area of trees larger than the subject tree ($\text{m}^2 \text{ ha}^{-1}$) and $\varepsilon_{d,i,t}$ and $\varepsilon_{h,i,t}$ is the normally distributed random error term of the diameter and height models respectively. a_0 – a_4 , b_0 – b_5 , and c_0 – c_2 are parameters to be estimated. Further, k_1 is a parameter estimated from data that allows growth for $d_{i,t} = 0$ and k_2 is a constant equal to 1 that ensures a positive denominator for small trees.

As with the stand-level model (Paper II) the individual-tree growth model was estimated by iteratively projecting each observed value (diameter or height) to the next, minimizing the squared deviations at the end of the measurement interval. A special problem was related to estimation of the individual-tree growth model as interim values of G and G_L between measurements could not be updated based on the predicted values of d as an intrinsic part of the estimation procedure. This was solved by an iterative procedure where predicted interim values of G and G_L were calculated from initial parameter guesses and then used to obtain improved parameter estimates. The procedure was repeated until convergence. In another study on individual-tree growth models (Paper V), the problem of quantifying the simultaneous interactions among individual trees was solved by combining n individual equations simultaneously for the n modelled trees. However this approach was practically infeasible due to the size of the dataset used for estimation of this model.

The complexity of estimation techniques applied when estimating individual-tree growth has increased with the increasing complexity of the models. Most data for studying individual-tree growth contain repeated measurements of the individual trees. Due to correlations between individual measurements on the same tree, ordinary least squares estimation will lead to negative bias of the covariance matrix and thus biased estimates of parameter variance. In a series of studies, generalized least squares and maximum

likelihood techniques has been applied to deal with such correlations (Newberry and Burkhardt, 1986; Gregoire, 1987; West, 1995). In the present study, serial correlations were modelled explicitly by a first-order autoregressive model that accommodates the irregular spacing of measurements:

$$\varepsilon_{m,j} = \rho_m^{t_j - t_{j-1}} \varepsilon_{m,j-1} + u_{m,j} \quad (i = 1, 2, \dots), \quad (3.21)$$

In a study of individual-tree growth of Norway spruce, cross-equation correlations between models describing basal area and height growth was observed (Hasenauer et al., 1998). The presence of such correlations indicated that OLS estimation would lead to biased estimates which were eliminated by three-stage least-squares estimation of the simultaneous equations. In a similar study of white spruce in mixed-species stands, individual equations were found to be correlated and the three-stage procedure was found to be more efficient in estimating the simultaneous system of equations than both a two-stage procedure and seemingly unrelated regression (Huang and Titus, 1999). However, when error correlations are small the improvement resulting when including those correlations in the estimation procedure may very well be outweighed by the loss of data that occurs because heights are measured more infrequently than diameters. As the correlation coefficient between errors of the diameter and height models were only 0.08, the equations were treated individually.

Initially, model parameters a_0 and b_0 were estimated locally for each experiment as a measure of site quality whereas the remaining parameters were estimated globally. The local parameter estimates were highly correlated with the rate constant of the stand-level model (Paper II) and with site index (Paper I), but were uncorrelated with soil texture variables such as fractions of clay, silt, sand, and coarse sand. Model parameters were subsequently estimated using the rate constant of the stand model as well as estimated site index as indicators of site quality.

The resulting system of individual-tree models yielded predictions that were consistent with tree growth and mortality expected for beech in Denmark. Although the results indicate that some model bias is still present, the systematic deviations from the observed mean were small.

Adding a stochastic element to the individual-tree model Plant populations are characterized by variability among individuals due to both intrinsic differences between individuals and environmental effects on individual plant growth. As a result of the stochasticity of plant growth, deterministic models, such as the individual-tree model presented here, may fail to mimic the tree size differentiation process over time and impede accurate prediction of size distributions. To illustrate this point, consider a theoretical stand of n uniformly dispersed trees of exactly the same size. Projecting such a stand into the future, using a deterministic individual-tree model,

will yield a series of forecasts in which the trees have the same relative size. This is of course wrong since genetic differences and random environmental impacts on the stand would lead to size differentiation.

The effect of variability in plant growth on the dynamics of the size distribution pattern can be analyzed by stochastic modelling of individual plant growth (Hara, 1984). The stochastic element may be added to the deterministic regression equation as a random component and is often assumed to be normally distributed with zero mean and variance equal to observed variance of periodic growth or to the residual mean square of the fitted regression (Gertner, 1987; Vanclay, 1991; Wichmann, 2002). Such models have been found to improve prediction accuracy of future size distributions (Tang et al., 1997; Wichmann, 2002) and allows for assessment of uncertainty of e.g. forecasts of size distributions or economic output in model applications.

Despite the apparent usefulness of a stochastic approach to individual-tree modelling there are only few examples of applications of such models (e.g. Pretzsch et al., 2002; Stage, 1973). One reason may be that the efficiency and simplicity of a deterministic model is demanded for many planning or forecasting purposes. Maybe more importantly, the estimation of the stochastic component requires extensive data that are most often not available to the modeller. In a preliminary study the individual-tree observations from permanent sample plots (see Chapter 2) was used to add a stochastic component to the individual-tree growth model presented in Paper IV.

The temporal development of the size distribution, $f(t, x)$, may be described by the forward Kolmogorov equation, also known as a diffusion equation (Hara, 1984; Kreyszig, 1999):

$$\frac{\partial f(t, x)}{\partial t} = -\frac{\partial f(t, x)}{\partial x}G(t, x) + \frac{1}{2}\frac{\partial^2 f(t, x)}{\partial x^2}D(t, x) - M(t, x)f(t, x), \quad (3.22)$$

where $G(t, x)$ is the drift coefficient, $D(t, x)$ is the diffusion coefficient and $M(t, x)$ is the termination coefficient of the diffusion process (Kreyszig, 1999). In terms of individual-tree growth the three intrinsic functions express increment (G), increment variation (D) and mortality (M) respectively for a tree of size x at the time t .

Equation (3.22) can only be solved analytically for very simple problems. Hence, as the intrinsic functions increase in complexity, the partial difference equation may be approximated numerically by the so-called implicit method, which involve estimation of the coefficients $G(t, x)$, $M(t, x)$, and $D(t, x)$ individually (Hara, 1984). In the present study, the growth and mortality functions were estimated as difference equations as described above and presented in Paper IV. Increment variance (D) for 2-cm diameter classes across all measurement occasions was approximated by the squared

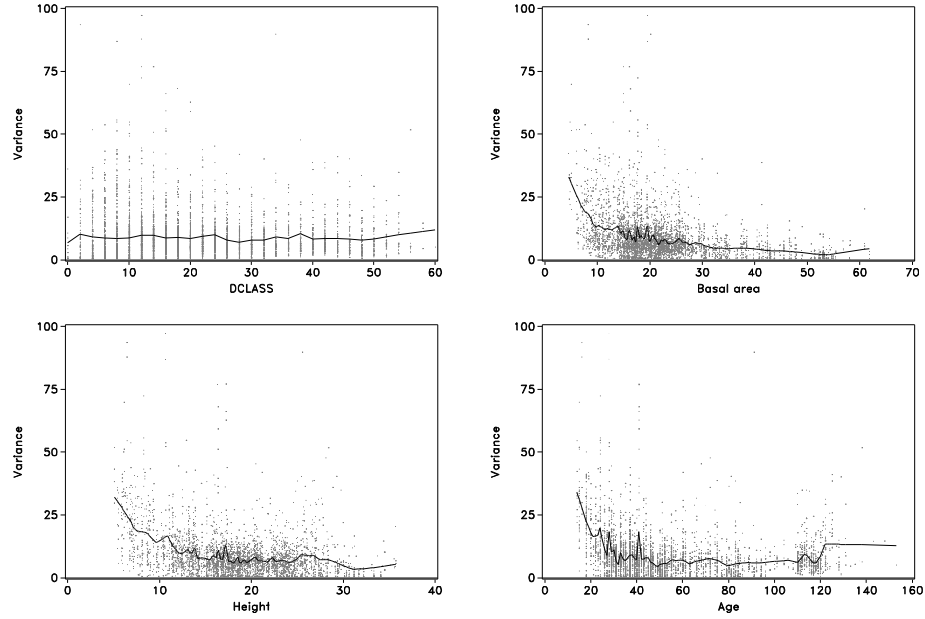


Figure 3.6: Increment variance calculated across plots and measurements as the standard deviation of the mean increment in each 2-cm diameter class. Black lines represent the LOESS-estimate of mean variance for different levels of stand basal area, dominant height and stand age.

standard deviation of mean annual increment between subsequent measurements (Figure 3.6). To avoid bias, variance estimates based on less than 10 observations were excluded from the analysis.

Based on a graphical interpretation of the increment variances depicted in Figure 3.6 and graphical representations of the variances estimated for individual plots a number of linear models were tested. The subject models were evaluated based on Akaike's Information Criteria (AIC) as well as their general biological interpretations. Based on this preliminary study the increment variance was estimated as:

$$D_t = \gamma_0 + \gamma_1 d_{i,t} + \gamma_2 d_{i,t}^2 + \gamma_3 H_{100,t} + \gamma_4 \ln(G_t) + \gamma_5 d_{i,t} H_{100,t} + \varepsilon_{i,t} \quad (3.23)$$

where $D_{i,t}$ is the increment variance of the i th tree at time t , and γ_1 – γ_5 are parameters to be estimated.

The increment variance model may be estimated by an ordinary least squares model to fit joint observations of variance and the estimators shown in equation (3.23). However, as the variance is positive and distributed:

$$S^2 \approx \sigma^2 \frac{\chi^2(df)}{df} \quad (3.24)$$

estimation of equation (3.23) is violating the assumption of normality. Hence, the model was estimated on the log-transformed variance.

The stochastic individual-tree model was evaluated by forecasting the temporal development of the diameter distribution by feeding initial size-distributions into equation (3.22) and then solving the equation numerically by the implicit method. Since the majority of stands in the data were managed, thinnings were modelled explicitly by removing individual trees according to the tree lists. The simulations were repeated 250 times to generate the mean diameter distribution. The generated distributions of trees to diameter classes of 1-cm width were compared to the observed distributions of each plot and measurement occasion by χ^2 -tests. Diameter classes of less than 5 predicted trees were combined with neighbouring classes to ensure the validity of the test.

The parameters of the increment variance model (equation (3.23)) indicated a greater increment variation in the large diameter-classes although the variation was decreasing as the trees grew older as indicated by the negative relation to the dominant height (Table 3.2). Further, variation was decreasing at increasing levels of competition indicated by basal area. The general conclusion from the obtained parameter estimates was that increment variance was generally increasing with expected absolute increment.

The increment variance model explained a little more than half of the observed variation in increment variance ($R^2=0.519$) and the residuals showed no apparent bias when plotted against the fixed or random effects of the model. Plotting the distribution of residuals of the increment variation model against the normal distribution indicated that the distribution is close to normal although statistical tests revealed significant deviations from normality. Similar tests conducted on the random effects indicated that the distribution of random effects is close to normal.

Simulation of the temporal development of diameter distributions showed that the diameter distribution may be forecasted to at least the following measurement occasion ($\leq 6-8$ years, $P \leq 0.05$). As the simulation period increases an increasing number of forecasts fail. In a similar study of the forward Kolmogorov equation, the diameter distribution of an uneven-aged beech stand was correctly forecasted for a 20-25 year period (Wichmann, 2002, pp. 79-89). However, when forecasting an even-aged stand of Sitka spruce (*Picea sitchensis* Bong. Carr.) forecasts failed after 10-15 years. Forecasts fail sooner for unthinned or young stands than for thinned or old stands. Trials with completely uniform, theoretical stands showed that the

Table 3.2: Parameter estimates of the diameter growth model (equation (3.18)), mortality model (equation (3.20)), and increment variance model (equation (3.23)). Parameters of the growth and mortality functions are identical to those presented in Paper IV. Standard errors of the parameter estimates are provided in italics. All parameters were highly significant ($P < 0.0001$).

Parameter ^a	0	1	2	3	4	5	k_1	k_2
Diameter model ($G(i, t)$)	-2.2864 ^b	0.9700	-0.0026	-0.0183	-0.2007		25.6174	1
	<i>0.1233^b</i>	<i>0.0224</i>	<i>5.2E-5</i>	<i>2.44E-4</i>	<i>0.0011</i>		<i>1.9325</i>	.
Mortality model ($M(i, t)$)	7.4247	-36.7827	-0.0876					
	<i>0.0204</i>	<i>0.3176</i>	<i>5.44E-4</i>					
Variance model ($D(i, t)$)	5.2564	0.1127	-0.0052	-0.2483	-0.6613	0.0087		
	<i>0.2179</i>	<i>0.0064</i>	<i>0.0002</i>	<i>0.0098</i>	<i>0.0930</i>	<i>0.0005</i>		

^aNumbers correspond to the suffix of the individual model parameters presented in equation (3.18), (3.20), and (3.23).

^bEstimated individually for each experiment, number represents a simple average.

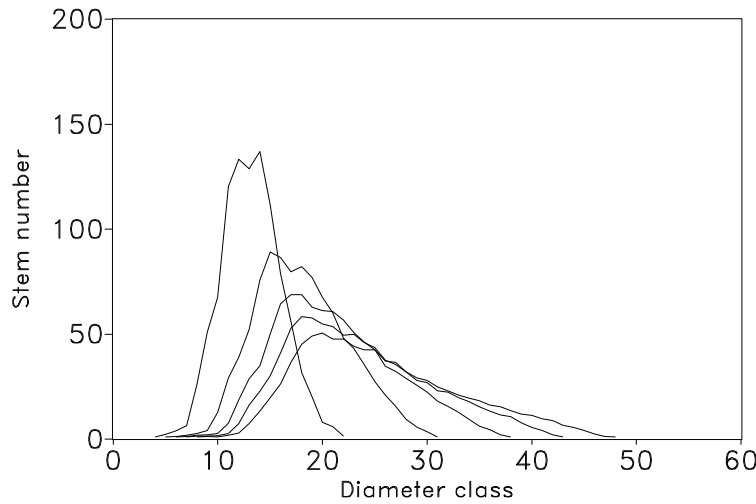


Figure 3.7: Simulation of the temporal development of the diameter distribution. At the beginning of the simulation, diameters were approximately distributed $N(10, 2^2)$.

stochastic model generated distributions with longer tails compared to the deterministic model. When the initial distribution of trees was normal, the predicted distribution became increasingly left skewed at increasing simulation period (Figure 3.7).

When comparing the simulated diameter distributions from the stochastic model with those from the corresponding deterministic model ($D(x) = 0$) a striking similarity is evident (an example is presented in Figure 3.8). Although the tails predicted from the stochastic model are longer than predicted by the deterministic model, the size distribution appears to be somewhat insensitive to the size differentiation process allowed by the stochastic model. Hence, the deterministic model may be sufficient for practical applications. The observed insensitivity of the model towards the increment variance is noted by a number of other authors (Kohyama and Hara, 1989; Kohyama, 1991, 1992; Wichmann, 2002) although the deterministic model was found to fail sooner than the stochastic when forecasting diameter distributions (Wichmann, 2002, pp. 79-89).

3.4.2 Quantifying individual-tree competition

In the article *Quantifying size-asymmetric growth among individual beech trees* (Paper V) individual-tree diameter and volume growth was modelled by a modified Richards-equation (Richards, 1959). The study was based on four different plots in experiment DQ on eastern Zealand. Two of the plots

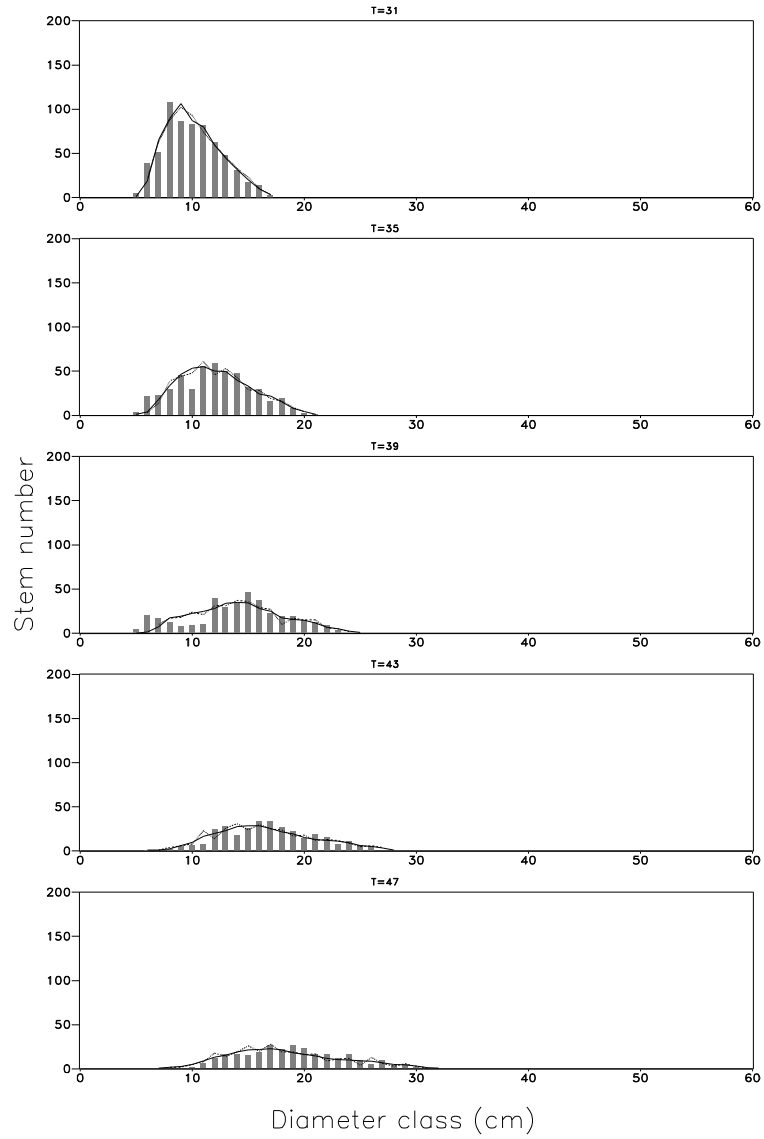


Figure 3.8: Observed (bars) vs. predicted (full line) diameter distributions at experiment EC for twenty years of simulations on the moderate thinning regime plot (B-grade). The dotted line represents the diameter distribution predicted by a deterministic model ($D(x) = 0$).

were thinned according to the ideas of Jagd, who advocated early, heavy thinnings ("Danish thinning", page 9), one plot was thinned according to those of Bavngaard, who advocated moderate thinnings at young ages and retention of understorey trees ("Funen thinning", page 9), and one plot was an unthinned control.

The growth of n competitively interacting trees was modelled by n coupled differential equations, where the absolute growth rate was a function of tree size and a parameter accounting for the degree of asymmetric growth (a). The effect of competition between plants within the population was modelled by the cumulative size of the n individual trees relative to the fitted maximum cumulative size of the n trees ($n\alpha$):

$$\frac{dv_i(t)}{dt} = \begin{cases} \frac{\kappa}{1-\delta} v_i(t)^a \left(\left(\frac{1}{n\alpha} \sum_{j=1}^n v_j(t) \right)^{\delta-1} - 1 \right) & \delta \neq 1 \\ \kappa v_i(t)^a \left(\ln(n\alpha) - \ln \left(\sum_{j=1}^n v_j(t) \right) \right) & \delta = 1 \end{cases} \quad (3.25)$$

where $v_i(t)$ is the size (volume and basal area) of tree i at time t , and κ , δ , α , and a are parameters to be estimated.

If $a = 0$, all trees have the same growth rate irrespective of their size (i.e. growth is completely symmetric). If $0 < a < 1$, the growth rate is less than proportional to the size of the tree. If $a = 1$, the growth rate is proportional to the size of the tree (i.e. growth is perfectly size-symmetric). If $a > 1$, the growth rate is more than proportional to the size of the tree and growth is size-asymmetric. If a is very large, only the largest trees grow and growth is completely asymmetric. Because the computational load increases rapidly with increasing number of trees, 100 trees were selected randomly from each plot for estimating the functions.

In diverse stands, a exceeded 1 and was larger in dense stands (control and Bavngaard-thinning) than in sparse stands (Jagd-thinning). This suggested that the predominant mode of competition was size-asymmetric and that this size-asymmetry increased with density.

In comparison to the individual-tree model presented in Paper IV, this article presented two novel features. Since a provides a measure of the relative importance of above- versus belowground competition, it may be useful in interpreting the growth dynamics of forest stands, and may provide additional information for modellers of forest growth. Further, the estimation of n simultaneous differential equations allow for explicit real-time modelling of plant interactions. Intuitively, this method simulates plant interactions more efficiently and the method thus represents an improvement to the iterative method for obtaining interim estimates of plant competition presented

in Paper IV. However, the method is very computing intensive (estimation of the model using only 100 trees took about one month per plot) and is thus not yet feasible when estimating general individual-tree growth models using large datasets.

3.4.3 A spatial individual-tree growth model

Compared to the vast amount of data available for non-spatial modelling of individual-tree growth in this study only a limited number of experiments (16) included spatial information on the individual trees. In accordance with the general thinning practise in Denmark these stands were all relatively homogenous and thus represented a limited range of the possible stand structures. Hence, the competitive interactions of heterogeneous stands would most likely not be captured by models estimated on this data and the material in general seemed unsuited for making spatial individual-tree growth models. However, the ongoing conversion to near-natural forestry has generated a demand for spatial models as non-spatial models may not be expected to be feasible for the future heterogeneous forest structures. Thus, in the article *A spatially explicit individual-tree model* (Paper VI) a preliminary study is conducted to assess the importance of the spatial arrangement of individual trees when modelling growth.

Various spatial individual-tree growth models were estimated and their predictions were compared with those of a non-spatial model. The hypothesis tested in this study was that the spatial arrangement of individual trees influences individual-tree growth, and that spatial competition indices more appropriately express competition and hence results in better estimates of individual-tree growth. The model tested was a linearized, mixed-effects version of the diameter increment model presented in Paper IV:

$$\ln(\Delta d_{i,j,t}) = \beta_1 + \beta_2 \ln(d_{i,j,t}) + \beta_3 d_{i,j,t} + \beta_4 CI_{i,j,t} + u_j + v_i + \varepsilon_{i,j,t} \quad (3.26)$$

where $d_{i,j,t}$ is the diameter of the i th tree, at the j th plot at time t , $\Delta d_{i,j,t}$ is periodic annual diameter increment, $u_j \sim N(0, \sigma_p^2)$ and $v_i \sim N(0, \sigma_t^2)$ are the random effects of plots and individual trees, $\varepsilon_{i,j,t} \sim N(0, \sigma^2)$ is the "white noise", $\beta_1 - \beta_4$ are parameters to be estimated and CI_i is some measure of competition for the individual tree. Among the different indices those developed by Hegyi (1974) (H), Martin and Ek (1984) (ME), Bella (1971) (B), and Schneider et al. (2005) (L) were chosen for this study:

$$CI_H = \sum_{i \neq j} e_i \frac{d_j}{d_i(Dist_{ij} + 1)} \quad (3.27)$$

$$CI_{ME} = \sum_{i \neq j} e_i \frac{d_j}{d_i} \exp\left(\frac{-16Dist_{ij}}{d_i + d_j}\right) \quad (3.28)$$

$$CI_B = \sum_{i \neq j} e_i \frac{O_{ij}d_j}{Z_i d_i} \quad (3.29)$$

$$CI_L = \sum_{i \neq j} e_i \frac{O_{ij}}{2} (1 + \tanh(\rho(r_j - r_i))) \quad (3.30)$$

Bayesian posterior probability distributions of the parameters were calculated using the Metropolis-Hastings algorithm assuming an uninformative uniform prior distribution (Carlin and Louis, 1996, pp. 33-37). The posterior distributions were based on 50,000 samples with a burn-in period of 10,000 iterations for stabilizing parameter values. The parameters of equation (3.26) were estimated for a NULL model where no competition effect was included in the model, for a non-spatial model, and for the different spatial competition indices.

Results indicated that although models including some form of competition (spatial or non-spatial) performed better than the NULL model, spatial models did not perform better than the non-spatial model. This result was discussed in relation to the error structure of spatial models and perspectives for future research are outlined.

3.4.4 Application of the non-spatial individual-tree model

The individual-tree model presented in Paper IV may be used in simulation studies of individual-tree growth based on a list of trees. Based on the global parameter estimates, the site-specific parameters a_0 and b_0 may be estimated from repeated individual-tree measurements. Alternatively, model predictions may be based on either an estimate of the rate constant (α_0) of the dominant height growth model (Paper II) or on estimated site index. Simulation of individual-tree growth entails a series of distinct steps:

1. Simulate thinning by removing the desired stems from the list
2. Calculate basal area (G) and basal area of trees larger than each subject tree (G_L)
3. Based on present tree size, G_L , and G calculate diameter and height increment
4. Calculate the diameter and height of each tree after one growth season

5. Repeat the procedure from step 2.

Although the model is non-spatial, it may be applied in a spatial way. In a recent study on optimal target diameter harvesting (Meilby and Nord-Larsen, in preperation), the model was applied on a 4.9 ha forest stand. Here the site-specific parameter was allowed to vary across the stand because of large variation in site quality. Further, the competition experienced by each tree was estimated within a circular neighbourhood with radius 30 m around each tree. This approach has limitations as the size of the influence zone is set arbitrarily, but the method worked very well for this data.

Consistent tree- and stand-level estimates In simulation studies of stand- and tree-level models the two levels of models often fail to produce consistent results. Compatible results are a desirable feature of multilevel models and were obtained for an integrated system of four different levels of growth models by Daniels and Burkhart (1988). While equation forms and variables that will mathematically collapse to lower levels of resolution may be preferable, they do not address the problem of linking already existing stand- and tree-level models. Further, individual-tree models are often found to be superior to disaggregating stand-level growth. As integrated systems of individual-tree and stand-level models disaggregate stand-level growth to obtain predictions on the individual-tree level, such equations may yield inferior results when predicting individual-tree growth (Ritchie and Hann, 1997).

Another approach towards obtaining consistency between stand- and tree-level predictions of basal area is to scale predicted diameters by the square root of the ratio between predicted basal area of the stand-level model (G) and the sum of individual-tree basal areas predicted by the individual-tree model (Johannsen, 1999):

$$\widehat{\widehat{d}}_{i,t} = \widehat{d}_{i,t} \sqrt{G / \left(\frac{\pi}{40,000} \sum_{i=1}^n \widehat{d}_{i,t}^2 \right)} \quad (3.31)$$

The above approach towards getting consistent estimates of basal area is rather simplistic and may potentially yield inconsistent estimates of mean diameter. Linking stand- and tree-level models Somers and Nepal (1994) provided an algorithm that ensured consistency of predicted basal area and average diameter, while maintaining the relative growth of individual trees. This algorithm is somewhat more complex than the solution presented in equation (3.31) and can only be solved through iteration, but solves most of the problems of inconsistent estimates from the individual-tree and stand-level models.

Chapter 4

Conclusions and perspectives

The previous chapters have presented a series of forest growth and yield models, operating at different levels of resolution. The site-index curve, stand-level, and diameter distribution models are suited for applications in forest management, as tools for decision making, or in forest research. At present, the individual-tree growth models may have limited scope for forest management because of the data requirements, but they may have considerable scope for forest research, especially research focusing on the ongoing conversion towards near-natural forestry.

Simulating is a powerful tool for evaluating the development of stand structures, expected economic returns, etc. of near-natural forestry. However, the inference from such studies is only as strong as the data underlying the applied models and their proper accommodation of interactions determining growth. Unfortunately, the data underlying the models developed in this study were essentially even-aged and monospecific, which ultimately limit the applicability of the models for simulating the more heterogeneous stand structures of near-natural forestry. Furthermore, the models did not include multiple sources of stochasticity inherent in the data and originating from variable, unobserved environmental factors such as climate. Hence, there remains a need for collecting growth and yield data from uneven-aged stands and a considerable scope for further research on the development of growth models for uneven-aged management.

Recently, the advantages of Bayesian hierarchical models for modelling ecological time-series data has been convincingly demonstrated (Clark and Bjørnstad, 2004; Schneider et al., 2005). In a hierarchical statistical model, the effect of measurement error is distinguished from the effect of stochasticity (process error), giving unbiased parameter estimates. More importantly, by focusing on the measuring error and how the spatio-temporal variance is distributed among individuals it may become possible to integrate all the determining growth factors of individual plants in crowded populations. Furthermore, the Bayesian approach provides a good understanding of the

joint distribution of the biological parameters, giving us improved quantitative predictions in a more useful mathematical form, e.g. as probabilities of different outcomes or scenarios that may be useful for applied purposes.

Like many advances in science, new methods such as those proposed here often require data of a somewhat higher quality than earlier approaches. To model the growth of individuals in mixed-species and uneven-aged stands adequately, it is necessary to have sequential measurements of relevant variables from individuals in such populations for a major part of their life. Such data is not readily available in Denmark, where natural forest stands are generally absent except from the often measured near-natural Suserup Forest (Emborg et al., 2000) and the near-natural Draved Forest (Wolf, 2002). However, the Danish National Forest Inventory (Söderberg, 2000) may be a future source of data for modelling growth of trees and forests. In a 2x2 km grid covering all parts of Denmark, a cluster of plots are laid out at each grid point. Of the 3,000-3,500 plots on forest land, 30-40% of the plots are permanent from which spatial, individual-tree level data are collected. As this data cover the entire range of forest types in Denmark, including various mixtures of different species, it may be an excellent source of data for future advances in growth and yield modelling.

Bibliography

- Abell, J. and Jagd, T. (1954). Thinning problems and practices in Denmark. Technical publication 76, Syracuse State University, College of Forestry, New York. 92 p.
- Akaike, H. (1976). Canonical correlation analysis of time series and the use of an information criterion. In Mehra, R. K. and Lainotis, D. G., editors, *System identification: Advances and case studies*, pages 52–107. Academic Press, New York. 593 p.
- Amateis, R. L. and Burkhart, H. E. (1985). Site index curves for loblolly pine plantations on cutover site-prepared lands. *South. J. Appl. For.*, 9:166–169.
- Anonymous (2001). Teksten til danske retningslinier for bæredygtig skovdrift på ejendomsniveau. *SKOVEN*, 33:210–211.
- Assmann, E. (1961). *Waldertragskunde*. Bayerischen Landwirtschaftsverlag, München, Germany. 490 p.
- Badoux, E. (1939). De l'influence de divers modes et degrés d'éclaircie dans les hêtraies pures. *Mittellungen der Schweizerischen Anstalt für das Forstliche Versuchswesen*, 21:59–146.
- Bailey, R. L. (1980). Individual tree growth derived from diameter distribution models. *For. Sci.*, 26:626–632.
- Bailey, R. L. and Burgan, T. M. (1989). Fertilized midrotation-aged slash pine plantations - stand structure and yield prediction models. *South. J. Appl. For.*, 13:13–17.
- Bailey, R. L. and Cieszewski, C. J. (2000). Development of a well-behaved site-index equation: jack pine in north-central Ontario: comment. *Can. J. For. Res.*, 30:1667–1668.
- Bailey, R. L. and Clutter, J. L. (1974). Base-age invariant polymorphic site curves. *For. Sci.*, 20:155–159.

- Bailey, R. L. and Dell, T. R. (1973). Quantifying diameter distributions with the Weibull function. *For. Sci.*, 19:97–104.
- Bartelink, H. H. (2000). Effects of stand composition and thinning in mixed-species forests: a modeling approach applied to Douglas-fir and beech. *Tree Physiol.*, 20:399–406.
- Bella, I. E. (1971). A new competition model for individual trees. *For. Sci.*, 17:364–372.
- Bertalanffy, L. v. (1949). Problems of organic growth. *Nature*, 163:156–158.
- Bertalanffy, L. v. (1957). Quantative laws in metabolism and growth. *Quart. Rev. Biol.*, 32:217–231.
- Biging, G. S. and Dobbertin, M. (1992). A comparison of distance dependent competition measures for height and basal area growth of individual trees. *For. Sci.*, 38:695–720.
- Bliss, C. I. and Reinker, K. A. (1964). A lognormal approach to diameter distributions in even-aged stands. *For. Sci.*, 10:350–360.
- Bolker, B. M., Deutschman, D. H., Hartvigsen, G., and Smith, D. L. (1997). Individual-based modelling: what is the difference? *Trends in Ecology and Evolution*, 12:111.
- Borders, B. E. (1989). Systems of equations in forest stand modelling. *For. Sci.*, 35:548–556.
- Borders, B. E. and Bailey, R. L. (1986). A compatible system of growth and yield equations for slash pine fitted with restricted three-stage least squares. *For. Sci.*, 32:185–201.
- Borders, B. E., Bailey, R. L., and Clutter, M. L. (1988). Forest growth models: Parameter estimation using real growth series. In Ek, A. R., Shifley, S. R., and Burk, T. E., editors, *Forest growth modelling and prediction*, Proc. IUFRO conf. Vol. 2. USDA For. Serv. Gen. Tech. Rep. NC-120, pages 660–667. 1152 p.
- Borders, B. E. and Patterson, W. D. (1990). Projecting stand tables: A comparison of the Weibull diameter distribution method, a percentile-based projection method, and a basal area growth projection method. *For. Sci.*, 36:413–424.
- Bornebusch, C. H. (1920). Om Bedømmelse af Skovjordens Godhed ved Hjælp af Bundfloraen. *Dansk Skovforenings Tidsskrift*, 5:37–50.
- Bornebusch, C. H. (1923). Skovbundsstudier. *Det Forstlige Forsøgsvæsen i Danmark*, 8:1–148.

- Bornebusch, C. H. (1940). Udhugningens Betydning for Bøgeskovens Udformning og dens Værditilvækst. *Dansk Skovforenings Tidsskrift*, 16:261–320.
- Bravo, F., Hann, D. W., and Maguire, D. A. (2001). Impact of competitor species composition on predicting diameter growth and survival rates of Douglas-fir trees in southwestern Oregon. *Can. J. For. Res.*, 31:2237–2247.
- Brunner, A., Hahn, K., Biber, P., and Skovsgaard, J. P. (2006). Conversion of Norway spruce: A case study in Denmark based on silvicultural scenario modelling. In Hasenauer, H., editor, *Sustainable Forest Management – Growth Models for Europe*, pages 343–372. Springer, Berlin, Heidelberg, New York. 389 p.
- Brunner, A. and Nigh, G. (2000). Light absorption and bole volume growth of individual Douglas-fir trees. *Tree Physiol.*, 20:323–332.
- Bryndum, H. (1980). Bøgehugstforsøget i Totterup Skov. *Det Forstlige Forsøgsvæsen i Danmark*, 38:1–76.
- Burk, T. E. and Newberry, J. D. (1984). A simple algorithm for moment-based recovery of Weibull distribution parameters. *For. Sci.*, 30:329–332.
- Cajander, A. K. (1913). Über Walddtypen. *Acta Forestalia Fennica*, 1:1–175.
- Callesen, I. (2003). *Transfer functions for carbon sequestration, nitrogen retention and nutrient release capability in forest soils based on soil texture classification*. PhD thesis, Royal Veterinary and Agricultural University. Copenhagen, Denmark. 247 p.
- Cao, Q. V. (1993). Estimating coefficients of base-age-invariant site index equations. *Can. J. For. Res.*, 23:2343–2347.
- Cao, Q. V. (2000). Prediction of annual diameter growth and survival for individual trees from periodic measurements. *For. Sci.*, 46:127–131.
- Cao, Q. V. (2004a). Annual tree growth predictions from periodic measurements. Gen. Tech. Rep. SRS-71, U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC. 600 p.
- Cao, Q. V. (2004b). Predicting parameters of a Weibull function for modelling diameter distribution. *For. Sci.*, 50:682–685.
- Cao, Q. V. and Baldwin, V. C. (1999). A new algorithm for stand table projection models. *For. Sci.*, 45:506–511.
- Carbonnier, C. (1971). Bokens produktion i Södra Sverige. *Studia Forestalia Suecica*, 91:1–89.

- Carbonnier, C. (1975). Produktion i kulturbestand av ek i Södra Sverige. *Studia Forestalia Suecica*, 125:1–89.
- Carlin, B. P. and Louis, T. A. (1996). *Bayes and empirical Bayes methods for data analysis*. Chapman & Hall, London. 440 p.
- Carmean, W. H. (1956). Suggested modifications of the standard Douglas-fir site curves for certain soils in southwestern Washington. *For. Sci.*, 2:242–250.
- Casper, B. B. and Jackson, R. B. (1997). Plant competition underground. *Annu. Rev. Ecol. Syst.*, 28:545–570.
- Cescatti, A. and Piutti, E. (1998). Silvicultural alternatives, competition regime and sensitivity to climate in a European beech forest. *For. Ecol. Man.*, 102:213–223.
- Chen, W. J. (2004). Tree size distribution functions of four boreal forest types for biomass mapping. *For. Sci.*, 50:436–449.
- Christensen, M. and Emborg, J. (1996). Biodiversity in natural versus managed forests in Denmark. *For. Ecol. Man.*, 85:47–51.
- Cieszewski, C. J. (2001). Three methods of deriving advanced dynamic site equations demonstrated on inland Douglas-fir site curves. *Can. J. For. Res.*, 31:165–173.
- Cieszewski, C. J. (2003). Developing a well-behaved dynamic site equation using a modified Hossfeld IV function $y^3 = (ax^m)/(c+x^{m-1})$, a simplified mixed-model and scant subalpine fir data. *For. Sci.*, 49:539–554.
- Cieszewski, C. J. and Bailey, R. L. (2000). Generalized algebraic difference approach: theory based derivation of dynamic site equations with polymorphism and variable asymptotes. *For. Sci.*, 46:116–126.
- Clark, J. S. and Bjørnstad, O. N. (2004). Population time series; process variability, observation errors, missing values, lags, and hidden states. *Ecology*, 85:3140–3150.
- Clutter, J. L. (1963). Compatible growth and yield models for loblolly pine. *For. Sci.*, 9:354–371.
- Clutter, J. L. and Bennett, F. A. (1965). Diameter distribution in old-field slash pine plantations. Report 13, Ga. For. Res. Council. 9 p.
- Clutter, J. L., Fortson, J. C., v. Pienaar, L., Brister, G. H., and Bailey, R. L. (1992). *Timber management - a quantitative approach*, pages 30–62. Krieger Publishing Compagny, Florida. 333 p.

- Curtis, R. O. (1964). A stem-analysis approach to site-index curves. *For. Sci.*, 10:241–256.
- Curtis, R. O., DeMars, D. J., and Herman, F. R. (1974a). Which dependent variable in site index-height-age regressions? *For. Sci.*, 20:74–87.
- Curtis, R. O., Herman, F. R., and DeMars, D. J. (1974b). Height growth and site index for Douglas-fir in high-elevation forests of the Oregon-Washington Cascades. *For. Sci.*, 20:307–316.
- Czarnowski, M. S. (1964). Productive capability of locality as a function of soil and climate with particular reference to forest land. Biological Science Series 5, Louisiana State University Press, Baton Rouge. 174 p.
- Damgaard, C. (1999). A test of asymmetric competition in plant monocultures using the maximum likelihood function of a simple growth model. *Ecological Modelling*, 116:285–292.
- Damgaard, C. and Weiner, J. (2000). Describing inequality in plant size or fecundity. *Ecology*, 81:1139–1142.
- Damgaard, C., Weiner, J., and Nagashima, H. (2002). Modelling individual growth and competition in plant populations: growth curves of cheopodium album at two densities. *Journal of Ecology*, 90:666–671.
- Daniels, R. and Burkhardt, H. (1975). Simulation of individual tree growth and stand development in managed loblolly pine plantations. Technical Report FWS-5-75, Div. For. Wild. Res., Virginia Polytechnic and State University, Blacksburg, VA. 69 p.
- Daniels, R. F. (1976). Simple competition indices and their correlation with annual loblolly pine tree growth. *For. Sci.*, 22:1230–1237.
- Daniels, R. F. and Burkhardt, H. E. (1988). An integrated system of forest stand models. *For. Ecol. Man.*, 23:159–177.
- Daubenmire, R. (1976). The use of vegetation in assessing the productivity of forest lands. *The Bot. Rev.*, 42:115–143.
- de Liocourt, F. (1898). De l'aménagement des sapinières. Bulletin trimestriel 4, Société Forestière de Franche-Comté et Belfort. 645 p.
- Dent, J. B. and Blackie, M. J. (1979). *Systems Simulation in Agriculture*, pages 94–117. Applied Science Publishers ltd., London. 180 p.
- Durbin, J. and Watson, G. S. (1950). Testing for serial correlation in least squares regression i. *Biometrika*, 37:409–428.

- Eichhorn, F. (1904). Beziehungen zwischen Bestandeshöhe und Bestandesmasse. *Allg. Forst. Jagdztg.*, 80:45–49.
- Ek, A. R. (1974). Nonlinear models for stand table projection in northern hardwood stands. *Can. J. For. Res.*, 4:23–27.
- Emborg, J. (1998). Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. *For. Ecol. Man.*, 106:83–95.
- Emborg, J., Christensen, M., and Heilmann-Clausen, J. (2000). The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. *For. Ecol. Man.*, 126:173–189.
- Farr, W. A. and Harris, A. S. (1979). Site index of Sitka spruce along the Pacific coast related to latitude and temperatures. *For. Sci.*, 25:145–153.
- Ferguson, J. S. and Leach, J. W. (1978). Generalized least squares estimation of yield functions. *For. Sci.*, 24:27–42.
- Flewelling, J. W. and Monserud, R. A. (2002). Comparing methods for modelling tree mortality. In Crookston, N. L. and Havis, R. N., editors, *Proceedings of the Second forest vegetation simulator conference*, pages 168–175. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Fox, J. C., Ades, P. K., and Bi, H. (2001). Stochastic structure and individual-tree growth models. *For. Ecol. Man.*, 154:261–276.
- Franz, F. (1971). Grundlage und Verfahren standortbezogener Leistungsschätzung. Forschungsberichte 2, Forstliche Forschungsanstalt München, Germany. 316 p.
- Freese, F. (1960). Testing accuracy. *For. Sci.*, 6:139–145.
- Freist, H. (1962). Untersuchungen über den Lichtungszuwachs der Rotbuche und seine Ausnutzung in Forstbetrieb. *Forstwissenschaftliches Centralblatt*, 17:1–78.
- Fritzbøgger, B. (1994). *Kulturskoven*. Gyldendal, Copenhagen, Denmark. 438 p.
- Frothingham, E. (1918). Height growth as a key to site. *J. For.*, 16:754–760.
- Frothingham, E. (1921). Classifying forest sites by height growth. *J. For.*, 19:1–14.
- Furnival, G. M., Gregoire, T. G., and Valentine, H. T. (1990). An analysis of three methods for fitting site-index curves. *For. Sci.*, 36:464–469.

- García, O. (1983). A stochastic differential equation model for height growth of forest stands. *Biometrics*, 39:1059–1072.
- García, O. (1994). The state-space approach in growth modelling. *Can. J. For. Res.*, 24:1894–1903.
- Gertner, G. Z. (1985). Efficient nonlinear model estimation: Its relationship to measurement interval. *For. Sci.*, 31:821–826.
- Gertner, G. Z. (1987). Approximating precision in simulation projections: An effective alternative to Monte Carlo simulations. *For. Sci.*, 33:230–239.
- Goelz, J. C. G. and Burk, T. E. (1992). Development of a well-behaved site index equation: jack pine in north central Ontario. *Can. J. For. Res.*, 22:776–784.
- Goelz, J. C. G. and Burk, T. E. (1996). Measurement error causes bias in site index equations. *Can. J. For. Res.*, 26:1585–1593.
- Gompertz, B. (1832). On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Phil. Trans. Roy. Soc. London*, 123:513–585.
- Gram, J. P. (1879). Om Konstruktion af Normal-Tilvækstoversigter, med særligt Hensyn til Iagttagelserne fra Odsherred. *Tidsskrift for Skovbrug*, 3:207–270. Denmark.
- Gram, J. P. (1889). Om Konstruktion af Normal-Tilvækstoversigter, med særligt Hensyn til Iagttagelserne fra Odsherred (II). *Tidsskrift for Skovbrug*, 11:97–151. Denmark.
- Gregoire, T. G. (1987). Generalized error structure for forestry yield models. *For. Sci.*, 33:423–444.
- Grøn, H. (1931). *Bidrag til den Almindelige Skovøkonomis Teori*. Levin & Munksgaards Forlag, Copenhagen, Denmark. 630 p.
- Gyldenfeldt, W. (1881). En Lokal Tilvæxtoversigt for Bøg. *Tidsskrift for Skovbrug*, 5:269–284.
- Gyldenfeldt, W. (1883). En Tilvæxtoversigt for Bøg paa 2det Kjøbenhavns Distrikt. *Tidsskrift for Skovbrug*, 6:1–46.
- Hafley, W. L. and Buford, M. A. (1985). A bivariate model for growth and yield prediction. *For. Sci.*, 31:237–247.
- Hafley, W. L. and Schreuder, H. T. (1977). Statistical distributions for fitting diameter and height data in even-aged stands. *Can. J. For. Res.*, 7:481–487.

- Hann, D. W. and Hanus, M. L. (2002a). Enhanced diameter-growth-rate equations for undamaged and damaged trees in Southwest Oregon. Research Contribution 39, Forest Research Lab, College of Forestry, Oregon State University. 54 p.
- Hann, D. W. and Hanus, M. L. (2002b). Enhanced height-growth-rate equations for undamaged and damaged trees in Southwest Oregon. Research Contribution 41, Forest Research Lab, College of Forestry, Oregon State University. 38 p.
- Hann, D. W. and Larsen, D. R. (1991). Diameter growth equations for fourteen tree species in southwest Oregon. Research Bulletin 69, Forest Research Lab, College of Forestry, Oregon State University. 18 p.
- Hann, D. W., Marshal, D. D., and Hanus, M. L. (2003). Equations for predicting height-to-crownbase, 5-year diameter-growth rate, 5-year height-growth rate, 5-year mortality rate, and maximum size density trajectory for Douglas fir and western hemlock in the coastal region of the Pacific Northwest. Research Contribution 40, Forest Research Lab, College of Forestry, Oregon State University. 83 p.
- Hannon, G. E., Bradshaw, R., and Emborg, J. (2000). 6000 years of forest dynamics in Suserup Skov, a seminatural Danish woodland. *Global Ecology & Biogeography*, 9:101–114.
- Hara, T. (1984). A stochastic model and moment dynamics of the growth and size distribution in plant populations. *J. theor. Biol.*, 109:173–190.
- Hasenauer, H., Monserud, R. A., and Gregoire, T. G. (1998). Using simultaneous regression techniques with individual-tree growth models. *For. Sci.*, 44:87–95.
- Hauch, L. A. (1908). Nattefrostens virkning i Ung Bøgeskov. *Det Forstlige Forsøgsvæsen i Danmark*, 2:1–28.
- Hauch, L. A. (1921). Faren ved Plukhugst i danske Skove. *Dansk Skovforenings Tidsskrift*, 6:161–168.
- Hegyi, F. (1974). A simulation model for managing Jack pine stands. In Fries, J., editor, *Growth models for tree and stand simulations*, pages 74–90. Royal College of Forestry, Stockholm, Sweden.
- Helles, F. and Linddal, M. (1952). Early Danish contributions to forest economics. *Journal of Forest Economics*, 3:87–103.
- Henriksen, H. (1988). *Skoven og dens dyrkning*. Nyt Nordisk Forlag Arnold Busck, Dansk Skovforening, København, Denmark. 664 p.

- Henriksen, H. A. (1952). Hugststyrke og produktion. *Dansk Skovforenings Tidsskrift*, 37:488–499.
- Henriksen, H. A. and Bryndum, H. (1996). Bøgeforyngelser i Stagsrode Skov. In Skovsgaard, J. P. and Morsing, M., editors, *Bøgeselvfornygelser i Østjylland*, The Research Series no. 13, pages 5–162. Danish Forest and Landscape Research Institute, Denmark. 215 p.
- Holm, M. (1979). Ansätze zur Verbesserung der Laubholzwirtschaft durch naturgemäßen Waldbau. *Forstarchiv*, 50:27–32.
- Holm, O. G. T. (1892). Tilvækstoversigt for Bøgehøjskov paa Grevskabet Langlands Distrikt. *Tidsskrift for Skovvæsen*, 4:177–180.
- Holmsgaard, E. (1955). Åringsanalyser af danske skovtræer. *Det Forstlige Forsøgsvæsen i Danmark*, 22:1–246.
- Holmsgaard, E. (1985). Self-pruning, formation of epicormic shoots etc. during 25 years in a non-thinned and two thinned plots of a thinning experiment in beech. *Det Forstlige Forsøgsvæsen*, 38:1–51.
- Holmsgaard, E. and Olsen, H. C. (1960). Vejrets indflydelse på bøgens frugtsætning. *Det Forstlige Forsøgsvæsen i Danmark*, 26:345–370.
- Holstener-Jørgensen, H. (1958). Physical soil investigations in Danish beech-stands. *Det Forstlige Forsøgsvæsen*, 25:93–224.
- Holten, A. (1894). Tilvækstoversigt for Bøgehøjskov i Fløjstrup Skov under Baroniet Vilhelmsborg. *Tidsskrift for Skovvæsen*, 6:43–47.
- Holten-Andersen, P. (1986). Økonomien i cyklisk bøgedyrkning. *Dansk Skovforenings tidsskrift*, 71:251–290.
- Holten-Andersen, P. (1989). Danish yield tables in the past century. *Det Forstlige Forsøgsvæsen i Danmark*, 42:71–145.
- Huang, S. and Titus, S. J. (1999). Estimating a system of nonlinear simultaneous individual tree models for white spruce in boreal mixed-species stands. *Can. J. For. Res.*, 29:1805–1811.
- Jakobsen, N. K. (1976). Natural-geographical regions of Denmark. *Geografisk Tidsskrift*, 75:1–7.
- Johannsen, V. K. (1999). *A growth model for oak in Denmark*. PhD thesis, Royal Veterinary and Agricultural University. Copenhagen, Denmark. 197 p.

- Johannsen, V. K. (2002). Selection of diameter-height curves for even-aged oak stands in Denmark. Dynamic growth models for Danish forest tree species, Working paper 16, Danish Forest and Landscape Research Institute, Hørsholm, Denmark. 70 p.
- Kennel, R. (1972). Die Buchendurchforstungsversuche in Bayern von 1870 bis 1970. Forschungsberichte 7, Forstliche Forschungsanstalt München, München, Germany. 264 p.
- Knowe, S. A., Foster, G. S., Roussau, R. J., and Nance, W. L. (1994). Eastern cottonwood clonal mixing study: predicted diameter distributions. *Can. J. For. Res.*, 24:405–414.
- Knowe, S. A. and Stein, W. I. (1995). Predicting the effects of site preparation and protection on development of young Douglas-fir plantations. *Can. J. For. Res.*, 25:1538–1547.
- Knox, R. G., Peet, R. K., and Christensen, N. (1989). Population dynamics in loblolly pine stands: changes in skewness and size inequality. *Ecology*, 70:1153–1166.
- Kohyama, T. (1991). Simulating stationary size distribution of trees in rain forests. *Ann. Bot.*, 68:173–180.
- Kohyama, T. (1992). Size-structured multi-species model of rain forest trees. *Functional Ecology*, 6:206–212.
- Kohyama, T. and Hara, T. (1989). Frequency distribution of tree growth rate in natural forest stands. *Ann. Bot.*, 64:47–57.
- Korol, R. L., Miner, K. S., and Running, S. W. (1996). Testing a mechanistic model for predicting stand and tree growth. *For. Sci.*, 42:139–153.
- Kreyszig, E. (1999). *Advanced engineering mathematics*. John Wiley & Sons Inc, New York, 8th edition. 1156 p.
- Larsen, J. B. (1997). Skovbruget ved en skillevej – teknologisk rationalisering eller biologisk optimering? *Dansk Skovbrugs Tidsskrift*, 82:277–308.
- Larsen, J. B. and Madsen, P. (2001). Naturnær skovdrift – erfaringer, status for forskningen og muligheder i Danmark. Skovbrugsserien 29, Danish Forest and Landscape Research Institute, Hørsholm, Denmark. 51 p.
- Larsen, P. H. and Johannsen, V. K. (2002). *Skove og Plantager 2000*. Statistics Denmark, Centre for Forest, Landscape and Planning, Danish Forest and Nature Agency, Denmark. 171 p.

- Leary, R., Nimerfro, K., Brand, M. H. G., Burk, T., Kolka, R., and Wolf, A. (1997). Height growth modelling using second order differential equations and the importance of initial height growth. *For. Ecol. Man.*, 97:165–172.
- Lemmon, P. E. and Schumacher, F. X. (1962a). Stocking density around ponderosa pine trees. *For. Sci.*, 8:397–402.
- Lemmon, P. E. and Schumacher, F. X. (1962b). Volume and diameter growth of Ponderosa pine trees as influenced by site index, density, age, and size. *For. Sci.*, 8:236–249.
- Lenhart, J. D., Hunt, E. V., and Blackard, J. A. (1986). Site index equations for loblolly and slash pine plantations on non-old-fields in east Texas. *South. J. Appl. For.*, 10:109–112.
- Linder, M. (2000). developing adaptive forest management strategies to cope with climate change. *Tree physiol.*, 20:299–307.
- Lindquist, B. (1931). Den Skandinaviska bogskogens biologi. *Svenska Skogsvårdsforeningens Tidskrift*, 29:179–532.
- Liu, C., Zhang, L., Davis, C. J., Solomon, D. S., and Gove, J. (2002). A finite mixture model for characterizing the diameter distribution of mixed-species forest stands. *For. Sci.*, 48:653–661.
- Lorenz, M. O. (1905). Methods for measuring the concentration of wealth. *American Statistics Association*, 9:209–219.
- Lorimer, C. G. (1983). Tests of age-independent competition indices for individual trees in natural hardwood stands. *For. Ecol. Man.*, 6:343–360.
- Lynch, T. B. and Moser Jr., J. W. (1986). A growth model for mixed species stands. *For. Sci.*, 32:697–706.
- MacKinney, A. L. and Chaiken, L. E. (1939). Volume, yield, and growth of loblolly pine in the mid-atlantic coastal region. Tech. Note 33, U.S. Dep. Agric. For. Serv., Appalachian For. Exp. Stn., Asheville, N.C. 30 p.
- Madsen, E. M. and Pedersen, H. C. (2002). Udrensning i meget planterige bøgeforyngelser. *Dansk Skovbrugs Tidsskrift*, 87:109–130.
- Madsen, S. F. (1987). Volume equations for some important Danish forest tree species. *Det Forstlige Forsøgsvæsen*, 40:47–242.
- Magnussen, S. (1983). En tilvækstoversigt for rødgran på østersønære lerede morænejorde. *Dansk Skovforenings Tidsskrift*, 68:215–247.
- Mäkelä, A., Sievänen, R., Lindner, M., and Lasch, P. (2000). Application of volume growth and survival graphs in the evaluation of four process-based forest growth models. *Tree Physiol.*, 20:347–355.

- Martin, G. L. and Ek, A. R. (1984). A comparison of competition measures and growth models for predicting plantation red pine diameter and height growth. *For. Sci.*, 30:731–743.
- Matney, T. G. and Sullivan, A. D. (1982). Compatible stand and stock tables for thinned and unthinned loblolly pine stands. *For. Sci.*, 28:161–171.
- McDill, M. E. and Amateis, R. E. (1992). Measuring forest site quality using the parameters of a dimensionally compatible height growth function. *For. Sci.*, 38:409–429.
- McDill, M. E. and Amateis, R. E. (1993). Fitting discrete-time dynamic models having any time interval. *For. Sci.*, 39:499–519.
- Meyer, H. (1933). Eine matematisch-statistische Untersuchung über den Aufbau des Plenterwaldes. *Schweizerische Zeitschrift für Forstwesen*, 84:33–46, 88–103, 124–133.
- Meyer, H. (1940). A mathematical expression for height curves. *J. For.*, 38:415–420.
- Miina, J. (1993). Residual variation in diameter growth in a stand of Scots pine and Norway spruce. *For. Ecol. Man.*, 58:111–128.
- Mitscherlich, E. A. (1919). *Landwirtschaftliche Jahrbücher*, 53:167–182.
- Møller, C. M. (1929). Opstilling af Tilvækstoversigter ved hjælp af Regnestok og ren grafisk Udjævning. *Dansk Skovforenings Tidsskrift*, 14:249–281.
- Møller, C. M. (1933). Boniteringstabeller og Bonitetsvise Tilvækstoversigter for Bøg, Eg og rødgran i Danmark. *Dansk Skovforenings Tidsskrift*, 18:537–623.
- Møller, C. M. (1965). *Vore Skovtræarter og deres dyrkning*. Dansk Skovforening, København, Denmark. 552 p.
- Møller, C. M. and Holmsgaard, E. (1947). Svag Hugst, stærk Hugst og Hugst fra Toppen. *Dansk Skovbrugs Tidsskrift*, 32:393–445.
- Møller, C. M. and Nielsen, J. (1953). Afprøvning af de Bonitetsvise Tilvækstoversigter af 1933 for Bøg, Eg og Rødgran i Danmark. *Dansk Skovbrugs Tidsskrift*, 38:1–167.
- Moltesen, P. (1988). *Skovtræernes ved og dets anvendelse*. Skovteknisk Institut, Frederiksberg, Denmark. 132 p.
- Monserud, R. A. (1976). Simulation of forest tree mortality. *For. Sci.*, 22:438–444.

- Monserud, R. A. (1984). Height growth and site-index curves for inland Douglas-fir based on stem analysis data and forest habitat type. *For. Sci.*, 30:943–965.
- Monserud, R. A. (1986). Time-series analyses of tree ring chronologies. *For. Sci.*, 32:349–372.
- Monserud, R. A. and Sterba, H. (1996). A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. *For. Ecol. Man.*, 80:57–80.
- Monserud, R. A. and Sterba, H. (1999). Modelling individual tree mortality for Austrian forest species. *For. Ecol. Man.*, 113:109–123.
- Näslund, M. (1936). Skogsforsöksastaltens gallringsforsök i tallskog. *Meddelanden från Statens Skogsforsöksanstalt*, 29:1–169.
- Naumann, A. and Julich, L. (1997). Berücksichtigung von Rot- und Spritzkernen bei der Holznutzung. *Allgemeine Forstzeitschrift für Waldwirtschaft und Umweltvorsorge*, 49:528–531.
- Nelson, T. C. (1964). Diameter distribution and growth of loblolly pine. *For. Sci.*, 10:105–114.
- Nepal, S. K. and Somers, G. L. (1992). A generalized approach to stand table projection. *For. Sci.*, 38:120–133.
- Newberry, J. D. and Burkhart, H. E. (1986). Variable-form stem profile models for loblolly pine. *Can. J. For. Res.*, 16:109–114.
- Newnham, R. M. and Smith, J. H. G. (1964). Development and testing of stand models for Douglas fir and lodgepole pine. *For. Chron.*, 40:494–502.
- Newton, P. F. and Jolliffe, P. (1998). Assessing processes of intraspecific competition within spatially heterogeneous black spruce stands. *Can. J. For. Res.*, 28:259–275.
- Newton, P. F., Lei, Y., and Zhang, S. Y. (2005). Stand-level diameter distribution yield model for black spruce plantations. *For. Ecol. Man.*, 209:181–192.
- Nord-Larsen, T., Bechsgaard, A., Holm, M., and Holten-Andersen, P. (2003). Economic analysis of near-natural beech stand management in northern Germany. *For. Ecol. Man.*, 184:149–165.
- Opie, J. E. (1962). Predictability of individual tree growth using various definitions of competing basal area. *For. Sci.*, 14:314–323.

- Oppermann, A. (1887). *Bidrag til Det Danske Skovbrugs Historie*. Gyldendalske Boghandels Forlag, København, Denmark. 356 p.
- Oppermann, A. (1914). God dansk Bøgeskov, belyst ved tre Tilvækstoversigter. *Det Forstlige Forsøgsvæsen*, 4:341–377.
- Oppermann, A. and Bornebusch, C. H. (1926). *Fra Skov og Planteskole*. Ibidem, København, Denmark.
- Pardé, J. (1962). Sylviculture et Production du hêtre. *Notes Techniques forestières*, 15.
- Parker, H. (1942). Dominant height and average diameter as a measure of site quality. *For. Chron.*, 18:152–156.
- Payandeh, B. and Wang, Y. (1994). Relative accuracy of a new base-age invariant site index model. *For. Sci.*, 40:341–348.
- Petersen, B. H. (1967). Bøgens fremtid i Danmark. *Dansk Skovforenings Tidsskrift*, 52:116–139.
- Petersen, B. H. (1981). Erfaringer fra over 40 års virke på samme distrikt. *Dansk Skovforenings Tidsskrift*, 66:240–267.
- Petersen, B. H. (1982). Økonomisk bøgedyrkning. *Dansk Skovforenings Tidsskrift*, 67:60–68.
- Petrini, S. (1938). Boniteringstabeller för bok. *Meddelanden från Statens Skogsforsöksanstalt*, 31:65–86.
- Petterson, H. (1955). Barrskogens volumproduktion. *Meddelanden från Statens Skogsforskningsinstitut* 45:1, Statens Skogsforskningsinstitut, Stocholm, Sweden. 391 p.
- Pienaar, L. V. and Harrison, W. M. (1988). A stand table projection approach to yield prediction in unthinned even-aged stands. *For. Sci.*, 34:804–808.
- Pienaar, L. V. and Shiver, B. D. (1980). Dominant height growth and site index curves for loblolly pine plantations in the Carolina Flatwoods. *South. J. Appl. For.*, 4:54–59.
- Pretzsch, H. (1997). Analysis and modelling of spatial stand structures. Methodological considerations based on mixed beech-larch stands in Lower Saxony. *For. Ecol. Man.*, 97:237–253.
- Pretzsch, H., Biber, P., and Dürský, J. (2002). The single tree-based stand simulator SILVA: construction, application and evaluation. *For. Ecol. Man.*, 162:3–21.

- Prodan, M. (1953). Die Verteilung des Vorrates gleichaltriger Hochwaldbestände auf Durchmesserstufen. *Allgemeine Forst- und Jagdzeitung*, 124:93–106.
- Pukkala, T. (1989). Predicting diameter growth in even-aged Scots pine stands with a spatial and non-spatial model. *Silvia Fennica*, 23:101–106.
- Ratkowsky, S. A. (1983). *Nonlinear regression modelling*. Marcel Dekker, New York. 276 p.
- Reed, D. D. and Burkhart, H. E. (1985). Spatial autocorrelation of individual tree characteristics in loblolly pine stands. *For. Sci.*, 31:575–587.
- Rennolls, K. and Wang, M. (2005). A new parameterization of Johnson's S_B distribution with application to fitting forest tree diameter data. *Can. J. For. Res.*, 35:575–579.
- Reventlow, C. D. F. (1816). Formeentlige Resultater af en deel Fortsatte Undersøgelser angaaende indflydelsen af Træernes gjensidige Afstand på deres mere eller mindre Fordelagtige Vegetation. *Det Kongelige Danske Videnskabernes Selskabs skrifter for aar 1809, 1810, 1811 og 1812*. 3. Række, 6. Bind, II. Hæfte.
- Reventlow, C. D. F. (1879). *Forslag til en forbedret Skovdrift, grundet paa Undersøgelser over Træernes Vegetation i Danmarks og Slesvigs Skove*. P. Hauberg & Co, Kjøbenhavn. 206 p.
- Reynolds, M. R. (1984). Estimating the error in model predictions. *For. Sci.*, 30:454–469.
- Reynolds, M. R., Burk, T. E., and Huang, W.-C. (1988). Goodness-of-fit tests and model selection procedures for diameter distribution models. *For. Sci.*, 34:373–399.
- Richards, F. J. (1959). A flexible growth equation for empirical use. *Journal of Experimental Botany*, 10:290–300.
- Ritchie, M. W. and Hann, D. W. (1986). Development of a tree height growth model for Douglas-fir. *For. Ecol. Man.*, 15:135–145.
- Ritchie, M. W. and Hann, D. W. (1997). Evaluation of individual-tree and disaggregative prediction methods for Douglas-fir stands in western Oregon. *Can. J. For. Res.*, 27:207–216.
- Rowe, J. S. (1956). The use of undergrowth plant species in forestry. *Ecology*, 37:461–473.
- Rubner, K. (1921). Die Spätfroste und die Verbreitungsgrenzen unsere Waldbäume. *Forstwissenschaftliches Centralblatt*, 43:41–49.

- Rubner, K. (1960). *Die Pflanzengeographischen Grundlage des Waldbaus*. Neumann Verlag, Berlin, Germany. 620 p.
- Sabroe, A. S. (1967). Overstandere og deres undergivne. *Dansk Skovforenings Tidsskrift*, 52:29–67.
- Sands, P. J., Battaglia, M., and Mummery, D. (2000). Application of process-based models to forest management: experience with PRODMOD, a simple plantation productivity model. *Tree Physiol.*, 20:383–392.
- Sarkkola, S., Hökkä, H., Laiho, R., Päivänen, J., and Penttilä, T. (2005). Stand structural dynamics on drained peatlands dominated by Scots pine. *For. Ecol. Man.*, 206:135–152.
- SAS Institute Inc. (1993). *SAS/ETS[©] User's guide, version 6*. Cary, N.C., second edition. 554 p.
- Schneider, M. K., Law, R., and Illian, J. B. (2005). Quantification of neighbourhood-dependent plant growth by Bayesian hierarchical modelling. *Journal of Ecology*, In press.
- Schober, R. (1972). *Die Rotbuche 1971*. Saurländer's Verlag, Hannover, Germany. 333 p.
- Schreuder, H. T. and Hafley, W. L. (1977). A usefull bivariate distribution for describing stand structure of tree heights and diameters. *Biometrics*, 33:471–477.
- Schreuder, H. T., Hafley, W. L., and Bennet, F. A. (1979). Yield prediction for unthinned natural slash pine stands. *For. Sci.*, 25:25–30.
- Schwappach, A. (1893). *Wachstum und Ertrag normaler Rotbuchenbestände*. Preussichen Hauptstation des forstlichen Versuchswesens. Verlag von Julius Springer, Germany. 73 p.
- Schwappach, A. (1908). *Die Kiefer*. Mitteilungen aus dem forstlichen Versuchswesen Preussens. Verlag von J. Neumann, Germany. 180 p.
- Schwappach, A. (1911). *Die Rotbuche*. Mitteilungen aus dem forstlichen Versuchswesen Preussens. Verlag von J. Neudamm, Germany. 231 p.
- Schwinning, S. (1996). Decomposition analysis of competitive symmetry and size structure dynamics. *Annals of Botany*, 77:422–432.
- Schwinning, S. and Fox, G. A. (1995). Competitive symmetry and its consequences for plant population dynamics. *Oikos*, 72:422–432.
- Schwinning, S. and Weiner, J. (1998). Mechanisms determining the degree of size-asymmetry in competition among plants. *Oecologia*, 113:447–455.

- Scolforo, J. R. S., César, F., Tabai, V., de Macedo, R. L. G., Jr., F. W. A., and de Assis, A. L. (2003). S_B distributions's accuracy to represent the diameter distribution of *Pinus taeda*, through five different fitting methods. *For. Ecol. Man.*, 175:489–496.
- Seber, G. A. F. and Wild, C. J. (1989). *Nonlinear Regression*. Wiley series in probability and mathematical statistics. Wiley, New York. 768 p.
- Siipilehto, J. (1999). Improving the accuracy of predicted basal-area diameter distribution in advanced stands by determining stem number. *Silva Fennica*, 33:281–301.
- Simard, S. W. and Sachs, D. L. (2004). Assessment of interspecific competition using relative height and distance indices in an age sequence of seral interior cedar-hemlock forests in British Columbia. *Can. J. For. Res.*, 34:1228–1240.
- Skov- og Naturstyrelsen (1994). Redegørelse til Folketinget om en samlet dansk skovpolitik i lyset af Rio- og Helsinki konferencerne. Technical report, Miljøministeriet, Skov- og Naturstyrelsen, København.
- Skov- og Naturstyrelsen (2002). Danmarks nationale skovprogram. Technical report, Miljøministeriet, Skov- og Naturstyrelsen, København. 83 p.
- Skov- og Naturstyrelsen (2005). Handlingsplan for naturnær skovdrift i statsskovene. Technical report, Miljøministeriet, Skov- og Naturstyrelsen, København. 60 p.
- Skov- og Naturstyrelsen and Larsen, J. B. (2005a). Katalog over skovudviklingstyper i Danmark. Technical report, Miljøministeriet, Skov- og Naturstyrelsen, København. 47 p.
- Skov- og Naturstyrelsen and Larsen, J. B. (2005b). Naturnær skovdrift - idekatalog til konvertering. Technical report, Miljøministeriet, Skov- og Naturstyrelsen, København. 72 p.
- Skovsgaard, J. P. (1988). En introduktion til forstlige vækstmodeller. Projekt tyndingsfri drift, Working paper 8, Forest Institute, Royal Veterinary and Agricultural University, Copenhagen, Denmark. 79 p.
- Skovsgaard, J. P. (1997). *Tyndingsfri drift af sitkagran*. Forskningsserien no. 19. Forskningscentret for Skov & Landskab, Hørsholm, Denmark. 525 p.
- Skovsgaard, J. P. and Henriksen, H. A. (1996). Increasing site productivity during consecutive generations of naturally regenerated and planted beech (*Fagus sylvatica* l.) in Denmark. In Spiecker, H., Mielikäinen, K., Köhl,

- M., and Skovsgaard, J. P., editors, *Growth trends of European forests: Studies from 12 countries*, European Forest Institute. Research Report, Vol. 5., pages 89–97. Springer-Verlag, Berlin Heidelberg. 372 p.
- Söderberg, U. (2000). Designing a sample-based national forest inventory for denmark. Report 2, Demonstration of methods to monitor sustainable forestry EU/LIFE project 1998-2001. 27 p.
- Somers, G. L. and Nepal, S. K. (1994). Linking individual-tree and stand-level models. *For. Ecol. Man.*, 69:233–243.
- Spiecker, H., Mielikäinen, K., Köhl, M., and Skovsgaard, J. P., editors (1996). *Growth trends of European forests: Studies from 12 countries*. European Forest Institute. Research Report, Vol. 5. Springer-Verlag, Berlin Heidelberg. 372 p.
- Spurr, S. H. (1962). A measure of point density. *For. Sci.*, 8:85–96.
- Stage, A. A. and Wykoff, W. R. (1993). Calibrating a model of stochastic effects on diameter increment for individual-tree simulations of stand dynamics. *For. Sci.*, 39:692–705.
- Stage, A. R. (1973). Prognosis model for stand development. USDA For. Ser. Res. Pap. INT-137, USDA Forest Service, Intermountain Forest & Range Experiment Station, Ogden, Utah, Intermountain Forest & Range Experiment Station, Ogden, Utah. 32 p.
- Statistics Denmark (2006). Skov5: Hugsten i skove og plantager i Danmark efter område og træsort. <http://www.statistikbanken.dk/statbank5a/default.asp?w=1024>.
- Stephens, M. A. (1977). Goodness-of-fit for the extreme value distribution. *Biometrika*, 64:583–588.
- Stout, B. B. and Shumway, D. L. (1982). Site quality estimation using height and diameter. *For. Sci.*, 28:639–645.
- Stuhr, G. (1978). Über das Wachstum von Buchenbeständen in Schleswig-Holstein. *Forstarchiv*, 49:256–259.
- Sullivan, A. D. and Clutter, J. L. (1972). A simultaneous growth and yield model for loblolly pine. *For. Sci.*, 18:76–86.
- Tang, S. Z., Wang, Y. H., Zhang, L. J., and Meng, C. H. (1997). A distribution-independent approach to predicting stand diameter distribution. *For. Sci.*, 43:491–500.

- Tham, Å. (1988). Structure of mixed *Picea abies* (L.) Karst. and *Betula pendula* Roth. and *Betula pubescens* Ehrh. stands in south and middle Sweden. *Scandinavian Journal of Forest Research*, 3:355–370.
- Titterton, D. M., Smith, A. F. M., and Makov, U. E. (1985). *Statistical analysis of finite mixture distributions*. John Wiley & Sons. 243 p. Reprinted in 1992.
- Tomé, M. and Burkhart, H. E. (1989). Distance-dependent competition measures for predicting growth of individual trees. *For. Sci.*, 35:816–831.
- Vanclay, J. K. (1991). Compatible deterministic and stochastic predictions by probabilistic modelling of individual trees. *For. Sci.*, 37:1656–1663.
- Vanclay, J. K. (1994). *Modelling Forest Growth and Yield*. CAB International, Wallingford, United Kingdom. 312 p.
- Verhulst, P. F. (1845). Recherches mathématiques sur la loi d'accroissement de la population. *Nouv. mém. de l'Académie Royale des Sci. et Belles-Lettres de Bruxelles*, 18:1–41.
- Verhulst, P. F. (1847). Deuxième mémoire sur la loi d'accroissement de la population. *Mém. de l'Académie Royale des Sci., des Lettres et des Beaux-Arts de Belgique*, 20:1–32.
- von Baur, F. (1877). *Die Fichte in Bezug auf Ertrag, Zuwachs und Form*. Verlag von Julius Springer, Berlin, Germany. 103 p.
- von Gadow, K. (1984). Die Erfassung von Durchmesserverteilungen in gleichaltrigen Kiefernbeständen. *Forstwissenschaftliches Centralblatt*, 103:360–374.
- Vuokila, Y. (1966). Functions for variable density yield tables of pine based on temporary sample plots. *Communicationes Instituti Forestalis Fenniae*, 60:1–86.
- Wang, Y. and Payandeh, B. (1994). Application of the Kalman filter model in site index equation construction. *Can. J. For. Res.*, 24:1415–1418.
- Wang, Y. and Payandeh, B. (1995). A base-age invariant site index model for aspen stands in north central Ontario. *For. Ecol. Man.*, 72:207–211.
- Wang, Y. and Payandeh, B. (1996). Evaluating a dimensionally compatible height growth modelling approach. *For. Chron.*, 72:647–650.
- Warren, W. G. (1980). On removing the growth trend from dendrochronological data. *Tree Ring Bull.*, 40:35–44.

- Watkinson, A. R., Lonsdale, W. M., and Firbank, L. G. (1983). A neighbourhood approach to self-thinning. *Oecologia*, 56:381–384.
- WCED, editor (1987). *World Commission on Environment and Development: Our Common Future*. Oxford University Press, New York. 343 p.
- Weibull, W. (1951). A statistical distribution function of wide applicability. *Journal of Applied Mechanics*, 18:293–297.
- Weiner, J. (1985). Size hierarchies in experimental populations of annual plants. *Ecology*, 66:743–752.
- Weiner, J. (1990). Asymmetric competition in plant populations. *Trends in Ecology and Evolution*, 5:360–364.
- Weiner, J. and Fishman, L. (1994). Competition and allometry in *Kochia scoparia*. *Annals of Botany*, 73:263–271.
- Weiner, J., Kinsman, S., and Williams, S. (1998). Modelling the growth of individuals in plant populations: local density variation in a strand population of *Xanthium strumarium* (Asteraceae). *American Journal of Botany*, 85:1638–1645.
- Weiner, J. and Solbrig, O. (1984). The meaning and measurement of size hierarchies in plant populations. *Oecologia*, 61:334–336.
- Weiner, J. and Thomas, S. C. (1986). Size variability and competition in plant monocultures. *Oikos*, 47:211–222.
- Weiner, J. and Thomas, S. C. (1992). Competition and allometry in three species of annual plants. *Ecology*, 73:648–656.
- Weiner, J., Wright, D. B., and Castro, C. J. (1997). Symmetry of below-ground competition between *Kochia scoparia* individuals. *Oikos*, 79:85–91.
- West, P. W. (1981). Simulation of diameter growth and mortality in regrowth eucalypt forest of southern Tasmania. *For. Sci.*, 27:603–616.
- West, P. W. (1995). Application of regression analysis to inventory data with measurements of successive occasions. *For. Ecol. Man.*, 71:227–234.
- Wichmann, L. (2001). Annual variations in competition symmetry in even-aged Sitka spruce. *Annals of Botany*, 88:145–154.
- Wichmann, L. (2002). *Modelling the effects of competition between individual trees in forest stands*. PhD thesis, Royal Veterinary and Agricultural University. Copenhagen, Denmark. 112 p.

- Wiedemann, E. (1932). *Die Rotbuche 1931*. Mitteilungen der Preußischen Forstlichen Versuchsanstalt. Verlag M.u.H. Schaper, Hannover, Germany. 189 p.
- Wolf, A. (2002). *Tree dynamics in Draved Forest : a long-term study of a temperate deciduous forest in Denmark*. PhD thesis, The Royal Veterinary and Agricultural University, Department of Economics and Natural Resources. Copenhagen, Denmark. 161 p.
- Wolfram, S. (2003). *The Mathematica Book*. Cambridge University Press, Cambridge, United Kingdom, 4 edition. 1470 p.
- Wunch, K. (1996). Matematisk formulering af H.A. Henriksens og H. Bryndums tilvækstoversigter for bøg. In Skovsgaard, J. P. and Morsing, M., editors, *Bøgeskulturforyngelser i Østjylland*, The Research Series no. 13, pages 149–162. Danish Forest and Landscape Research Institute, Denmark. 215 p.
- Wykoff, W. R. (1990). A basal area increment model for individual conifers in the northern Rocky Mountains. *For. Sci.*, 36:1077–1104.
- Wyszomirski, T., Wyszomirska, I., and Jarzyna, I. (1999). Simple mechanisms of size distribution dynamics in crowded and uncrowded virtual monocultures. *Ecological modelling*, 115:253–273.
- Zeide, B. (1993). Analysis of growth equations. *For. Sci.*, 39:594–616.
- Zhang, L., Gove, J. H., Liu, C., and Leak, W. B. (2001). A finite mixture of two Weibull distributions for modeling the diameter distributions of rotated-sigmoid, uneven-aged stands. *Can. J. For. Res.*, 31:1654–1659.
- Zon, R. (1913). Quality classes and forest types. In *Proceedings of the Society of American Foresters*, pages 100–104.

Papers

Paper I

Developing dynamic site
index curves

Developing dynamic site index curves for European beech (*Fagus sylvatica* L.) in Denmark

Thomas Nord-Larsen ^{*1}

^{*}Royal Veterinary and Agricultural University
Forest & Landscape
Hørsholm Kongevej 11, DK-2970 Hørsholm, Denmark

Abstract

In base-age specific methodologies, assessment of base age and site index may be a problem when developing site curves from repeated measurements on permanent sample plot data. In most cases such data will not contain measurements at any base age that is common for all the sample plots and some sort of interpolation or even extrapolation would have to be applied to address this issue. Base-age invariant methodologies pose the desirable property of estimating the curves without prior arbitrary assumptions about values of the site indices. Presented here is the development of such base-age invariant site index curves for European beech (*Fagus sylvatica* L.) in Denmark, fitted to permanent sample plot data. The developed polymorphic dynamic site equations with variable asymptotes are based on the generalized algebraic difference approach (*GADA*), and the parameters of the model were estimated with correction for first order serial correlation.

Keywords: estimation, base-age invariant, Chapman-Richards.

Introduction

Some assessment of site quality is required for making meaningful forecasts of forest growth and yield. A vast number of studies have been devoted to the characterisation of site quality (e.g. Meyer, 1940; Parker, 1942; Curtis, 1964; Curtis et al., 1974a). Although wood production may be the best direct measure of site quality it is difficult to measure. Hence the bulk of these studies have focused on the height of dominant trees as the single measure most closely related to the production capacity of a given site (e.g. Eichhorn, 1904; Frothingham, 1918, 1921).

Most methods for evaluation of site quality using stand or tree heights involve the application of site index curves. Such curves depict a family of height development patterns, often referenced by the height achieved at some *base age*. Early work on such *site curves* were based on graphical methods, but almost all recent studies involve the fitting of mathematical equations

¹Corresponding author. E-mail: tnl@kvl.dk, Phone: (+45) 35281758, Fax: (+45) 35271517

using statistical procedures. The first applications of such procedures extended the graphical methods by developing guide curves. The guide curve is an average equation for the sample data. From this equation parallel lines are developed, often by simple multiplication, for different heights attained at the base age. This method produces anamorphic curves and allows for estimation of site curves specific for individual stands through the multiplication. More recent work involves the development of three-dimensional functions of the general form $H = f(t, S, \boldsymbol{\beta})$ where t is some age, S is the height at base age and $\boldsymbol{\beta}$ is a vector of parameters. Such functions are often called static or base-age specific models because they predict height as a function of age and a site index at a fixed base age obtained from a direct height measurement. Fitting of such three-dimensional models, irrespective of the model being base-age specific or base-age invariant, may provide numerous desirable characteristics that include (e.g. Carmean, 1956; Cieszewski and Bailey, 2000; Clutter et al., 1992):

1. Curves through the origin
2. Polymorphism
3. Variable asymptotes
4. Equality of site index and predicted height at base age
5. Theoretical interpretability

In the attempt to make sufficiently flexible model forms, the benefits of such models come at the expense of increasingly complex equations which may cause the model to become unsolvable for S . Hence, separate models must be developed to estimate height as a function of site index and base age and to estimate site index as a function of height at any age. Even with model forms solvable for S , estimation of separate height growth and site index equations may also be a necessity simply because the two models most likely fail to produce consistent results (Curtis et al., 1974a).

An additional problem associated with the use of base-age specific models can occur when dealing with data from permanent sample plots measured at irregular intervals. Unlike data from stem analyses, such data may not contain measurements at the desired base age for all sample plots which in turn calls for some sort of interpolation or even extrapolation procedure to determine site index from the data. When estimating site curves from permanent sample plot data, a more appealing approach may be the base-age invariant approach introduced by Bailey and Clutter (1974). These models unequivocally define the individual site curves from any age-height point on the curve. As such, no need exists for prior knowledge of site index, and site curves may be estimated from permanent sample plot data without any inter- or extrapolations.

The development of height growth models have a long tradition in Northern Europe and in Denmark. Early Danish height curves for beech were produced by Gram (1879), who estimated mathematical functions for the development of normal yield tables. A series of height growth curves were subsequently developed for beech by various authors (e.g. Gyldenfeldt, 1881; Holm, 1892; Holten, 1894; Oppermann, 1914). Møller (1933) refuted the use of mathematical models in site curve modelling and developed a number of site curves and yield tables for beech based solely on graphical methods. These remain the most commonly used site curves in Danish forestry today. Later works for beech in northern central Europe include Carbonnier (1971); Henriksen and Bryndum (1996); Schober (1972); Stuhr (1978). Despite the abundance of site curves developed for beech in this region, the applied methods have generally lacked statistical rigour and objectivity. As such, a need exists for development of new and perhaps more well-founded site curves for European beech in Denmark.

The aim of the current study is to demonstrate the development of site curves for European beech in Denmark based on permanent sample plot data. Based on the previous discussion, the study concentrates on the derivation of base-age invariant site curves to obtain consistency between site index and predicted height at base age and to avoid the problem of inter- or extrapolation to determine site index.

Materials

European beech is one of the most common forest tree species in central Europe, and in Denmark is situated at the northernmost part of its range. Covering 17% of the total forest area, it is the most common deciduous species in Denmark (Larsen and Johannsen, 2002) and also the most significant in economic terms. European beech is a climax species and regenerates naturally on most soil types. The average site index (base age 100 years) of beech in Denmark is 28 m (Larsen and Johannsen, 2002) and the optimal rotation age in traditional even-aged management is 100-130 years. Recently, beech silviculture has received a lot of attention since this species is viewed as the dominant species in the ongoing conversion towards uneven-aged management of the Danish forests.

The data for developing site curves for European beech in Denmark originate from 68 permanent spacing, species and thinning experiments and a total of 184 individual plots. Plot sizes vary between 0.07 and 2.65 ha with an average of 0.40 ha. The data were collected during the period from 1872 to 2004 and the stands were observed for 10 to 120 years. Despite the time-span, data collection on the permanent sample plots has been remarkably uniform. In the earliest measurements diameter readings were obtained at 1/20 tree height. After 1880 trees were generally marked permanently at

4.15 feet ($\sim 1.3\text{m}$), numbered and recorded individually, making it possible to follow the individual tree. In some cases however, trees were recorded in tally list to diameter classes of 1-inch width. The conversion to the metric system in 1902 had little influence on the measurement practices except in the few cases where trees were recorded in tally lists to diameter classes of 1-cm width. As such, the data presented here represents more than 120 years of comparable measurements.

The experiments are located in most parts of Denmark and cover a wide range of site and growth conditions. However, the majority are situated in the eastern parts of the country in which the growth conditions are more suitable for growing beech than the sandy soils in western Denmark. The data includes a total number of 1520 measurement occasions and represent a wide range of initial spacing and thinning treatments that range from unthinned controls to heavily thinned stands. The thinning treatments include A-, B-, C- and D-grade thinnings, where the D-grade is usually thinned to 50% of the unthinned control's basal area (A-grade) and the B- and C-grades residual basal area are equally spaced between A- and D-grades. Some plots have been managed according to other thinning strategies, such as group- or selection-thinning and others were managed according to the thinning strategy typical at the time.

Measurements of diameter are obtained by averaging two perpendicular calliper readings taken at breast height (1.3m) for each tree. Observations also include records on whether the tree is alive or dead at the time of measurement. Individual height of live trees was measured using a hypsometer and felled trees were measured on the ground using a tape measure. On average 32.9 tree height measurements were obtained per measurement occasion.

Based on the paired observations of diameter and height, height-diameter equations were developed for each plot and measurement combination using a modified Näslund-equation (Näslund, 1936; Johannsen, 2002):

$$h = 1.3 + \left(\frac{d}{\alpha + \beta \cdot d} \right)^3 \quad (\text{I.1})$$

where d is the diameter at breast height, h is the total tree height and α and β are parameters to be estimated. The equations were then used to estimate the height of trees not measured. Dominant height, defined as the mean height of the 100 thickest trees per hectare (H_{100}), was then calculated for each plot and measurement combination. In the few cases where stem numbers were less than 100 per hectare, H_{100} was estimated as the mean height. Table I.1 presents a summary of the data.

Table I.1: Summary statistics of dominant height H_{100} , age (T), quadratic mean diameter (D_g), stem number (N) and basal area (G).

Variable	Unit	N	Mean	Minimum	Maximum	Std. Dev.
H_{100}	m	1520	20.91	5.08	36.95	7.74
T	years	1520	60.97	14	211	38.07
D_g	cm	1520	26.83	2.70	90.57	17.84
N		1520	1369.99	0.49	24720.45	2293.18
G	$m^2 ha^{-1}$	1520	20.20	0.21	73.58	8.97

Methods

Base-age invariant methods fit the three-dimensional surface (age, height and site index) in a manner that directly estimates the site-specific effects as parameters from the fitting procedure. Development of base-age invariant equations was first done by Bailey and Clutter (1974) using the *Algebraic Difference Approach* (ADA). The method was subsequently used in a number of studies (e.g. Pienaar and Shiver, 1980; Amateis and Burkhart, 1985; Lenhart et al., 1986; Furnival et al., 1990) and was recently extended to a generalized form (*GADA*) by Cieszewski (2001, 2003); Cieszewski and Bailey (2000).

GADA includes the following steps:

1. Select the basic equation form. This step is often performed using base-age specific methods to evaluate how well the equation represents the data.
2. Identify the site-specific parameter in the basic equation. Although Bailey and Clutter (1974) in their original formulation of the *ADA* describe models where site index depends solely on one parameter, any number may be specified in the *GADA*.
3. Generalize the site-specific parameters in the equation as functions of X , where X is an unknown measure of site quality. This step separates the *GADA* from *ADA* since introducing a function for the site-specific parameter allows it to vary across sites.
4. Solve for X and substitute for the independent variables, t and H , the initial conditions, t_0 and H_0 . The X in the equation developed in step 3 is finally replaced by this solution for X .

Model development The flexible Chapman-Richards equation (Richards, 1959) has been used in a large number of studies of site curves (e.g. Cao, 1993; Goelz and Burk, 1992; Monserud, 1984; Payandeh and Wang, 1994).

Since this equation is well-known to forest science and because of its simplicity, yet generally recognized properties it serves well as an example as to initial basic equation form:

$$H(t) = \beta_1 \left(1 - e^{-\beta_2 t}\right)^{\beta_3} \quad (\text{I.2})$$

The choice of site-specific parameter depends on the equation itself. If β_1 is chosen as the site-specific parameter, Equation (I.2) may be formulated as:

$$H(t, X) = X \left(1 - e^{-\beta_2 t}\right)^{\beta_3} \quad (\text{I.3})$$

where $H(t, X)$ is the height at age t , X is a site specific parameter or a function of any parameters and β_2 and β_3 are parameters to be estimated. Rather than choosing a simple formulation of X as in this example, X may be any number of simultaneous site-specific parameters necessary to describe the desired curve shapes (Cieszewski and Bailey, 2000). The solution for X in Equation (I.3) is:

$$X = H(t, X) \left(1 - e^{-\beta_2 t}\right)^{-\beta_3} = H_0 \left(1 - e^{-\beta_2 t_0}\right)^{-\beta_3} \quad (\text{I.4})$$

where H_0 is the height at any specific age (t_0). Substituting X in Equation (I.3) with Equation (I.4) yields the difference equation form of the Chapman-Richards height-age function and completes the *GADA* (which in this simple case is identical to the *ADA*):

$$H(t, t_0, H_0) = H_0 \left(\frac{1 - e^{-\beta_2 t}}{1 - e^{-\beta_2 t_0}} \right)^{\beta_3} \quad (\text{I.5})$$

From Equation (I.5) it is evident that the height H at age t may be estimated from any pair of age-height observations (t_0, H_0). H_0 could be treated as a site index (S) at base age (t_0), and from any height-age pair of observations S can be calculated from:

$$H_0 = S = H_t \left(\frac{1 - e^{-\beta_2 t}}{1 - e^{-\beta_2 t_0}} \right)^{-\beta_3} \quad (\text{I.6})$$

Similar derivations of difference forms of the Chapman-Richards equation may be made for the parameters β_2 and β_3 to yield equations Equation (I.7) and (I.8), respectively:

$$H(t, t_0, H_0) = \beta_1 \left(1 - e^{-Zt}\right)^{\beta_3}, Z = \frac{\ln \left[1 - \left(\frac{H_0}{\beta_1}\right)^{\frac{1}{\beta_3}}\right]}{t_0} \quad (\text{I.7})$$

$$H(t, t_0, H_0) = \beta_1 \left(1 - e^{-\beta_2 t}\right)^Z, Z = \ln \left[\frac{H_0}{\beta_1} - (1 - e^{-\beta_2 t_0}) \right] \quad (\text{I.8})$$

The three different formulations of the Chapman-Richards equation are either anamorphic with variable asymptotes [Equation (I.5)] or polymorphic with fixed asymptotes [Equation (I.7) and (I.8)].

In addition to the different forms of the Chapman-Richards equation a large number of other base-age invariant site equations were tested in relation to this study (models presented by e.g. Bailey and Clutter, 1974; Pienaar and Shiver, 1980; Amateis and Burkhart, 1985; Lenhart et al., 1986; Furnival et al., 1990; Cieszewski, 2001, 2003). Among the models tested the best fit and most desirable properties (according to the list of nine characteristics presented by Goelz and Burk (1992)) was obtained by the three-parameter *GADA* formulation of the logistic site equation by Monserud (1984) presented by Cieszewski (2001, Equation (21)):

$$H = H_0 \frac{t^{\beta_1} (t_0^{\beta_1} R + \beta_2)}{t_0^{\beta_1} (t^{\beta_1} R + \beta_2)} \quad (\text{I.9})$$

where:

$$R = Z_0 + \left(Z_0^2 + \frac{2\beta_2 H_0}{t_0^{\beta_1}} \right)^{0.5}$$

$$Z_0 = H_0 - \beta_3$$

This equation is highly flexible and holds a number of desirable properties such as variable asymptotes and polymorphism. The derivation of this equation is not shown here and readers are referred to the original paper.

Analysis The different equations were all solved using nonlinear least squares techniques. For each of the three base-age invariant forms of the Chapman-Richards equation, the site-specific parameter (H_0) was estimated locally for each experiment while the other parameters were estimated globally. The properties of the three two-parameter equations were assessed from a graphical analysis of curve shapes and residuals.

Equation (I.9) was initially estimated using a base-age specific method (BS) in which height at base age was used as site index. Site indices of individual experiments were estimated through interpolation for plots not having observations at the specific base age. Plots that did not have measurements around the base age were excluded from this analysis (i.e. no extrapolation from the data was carried out). Further, Equation (I.9) was estimated using the base-age invariant method (BI) where H_0 is considered a parameter specific to each experiment. This method was further extended to model first- and second-order correlation. Since the spacing between individual measurements were highly irregular, the correlation between disturbances was assumed to decline exponentially with the time between measurements:

$$\varepsilon_i = \rho^{t_i-t_{i-1}}\varepsilon_{i-1} + \rho^{t_i-t_{i-2}}\varepsilon_{i-2} \cdots + \rho^{t_i-t_{i-l}}\varepsilon_{i-l} + a_i \quad (\text{I.10})$$

where ε_i is the error of the i th measurement, ρ is the autocorrelation, l is the number of lags in the model and a_i is the "white noise" $a_i \sim N(0, \sigma)$.

Performance of the different models was analysed by R^2 -statistics, root mean square of residuals (RMSE) and average absolute bias (AAB). Overall bias in the models was examined using simultaneous F-test (Dent and Blackie, 1979). Heteroscedasticity and unexplained trends in the residuals across age, predicted height and site index were evaluated using both graphs of the data and lack of fit statistics on different strata of the data. Autocorrelation of residuals was assessed by calculating Durbin-Watson statistics as well as the empirical autocorrelation ρ between residuals r at lag l :

$$\rho(l) = \frac{\sum_{i=1}^M \sum_{j=1}^{n_i-1} r_{ij}r_{i(j+1)}/N(l)}{\sum_{i=1}^M \sum_{j=1}^{n_i} r_{ij}^2/N(0)} \quad (\text{I.11})$$

Results

The three different forms of the Chapman-Richards equation assumed either a fixed asymptote [Equation (I.7) and (I.8)] or anamorphism [Equation (I.5)]. Although fit statistics only deviate little from that of Equation (I.9) (Table I.2), these restrictions result in less attractive properties of these two-parameter equations.

Equation (I.5) is anamorphic and yields predictions that greatly exaggerate dominant height on high site index sites (Figure I.1, first row). Assuming a fixed asymptote and allowing β_2 to vary in Equation (I.7) leads to a better fit and improved predictive properties with regards to extrapolation and estimation of height growth at young ages and for low site index sites (Figure I.1, second row; Table I.2). However, assuming a fixed asymptote across different site qualities may be dubious from a biological point of view. Finally, assuming a fixed asymptote and allowing β_3 to vary in Equation (I.8) results in overestimation of dominant height growth with increasing age (Figure I.1, third row).

Fitting Equation (I.9), using the base-age specific method resulted in an improved model fit compared to the two-parameter Chapman-Richards equations. However, the method resulted in ill-conditioned residuals (Figure I.2, first row) as a result of the assumption of the reference height being estimated without error. More importantly, the data for developing site curves did not contain measurements at any age common to all plots, nor did the plots share the same range of ages. Since no extrapolation from the data was made, reference heights could not be computed for a number of plots, regardless of the choice of base age. At the chosen base age of 50 years,

Table I.2: Parameter estimates for the three base-age invariant site equations based on the Chapman-Richards equation [Equations (I.5), (I.7) and (I.8)] and Equation (I.9) (Cieszewski, 2001). BS and BI refer to base-age specific and base-age invariant estimation method, respectively. AR1 refers to the inclusion of a first order serial correlation regime. The table includes fit statistics such as root mean square error (RMSE), R-square and average absolute bias (AAB).

Equation	Para.	Estimate	Std. Err.	t-stat	RMSE	R-square	AAB
(I.5)	β_2	0.0218	0.001	44.14	1.047	0.983	0.758
	β_3	0.3332	0.011	31.29			
(I.7)	β_1	36.0013	0.201	178.89	0.982	0.985	0.678
	β_3	1.7846	0.030	59.64			
(I.8)	β_1	35.0895	0.187	187.76	1.154	0.979	0.814
	β_2	0.0288	0.001	530.35			
(I.9) (BS)	β_1	1.8295	0.021	88.11	0.922	0.982	0.647
	β_2	13336.6	2709.9	4.92			
	β_3	32.669	1.3124	24.89			
(I.9)	β_1	1.7175	0.021	82.31	0.963	0.985	0.671
	β_2	8335.34	1904.8	4.38			
	β_3	35.1066	1.2325	28.48			
(I.9) (AR1)	β_1	1.7184	0.031	55.91	0.762	0.991	0.513
	β_2	4087.59	2228.9	1.83			
	β_3	36.8647	1.489	24.76			
	ρ_1	0.9485	0.006	154.68			

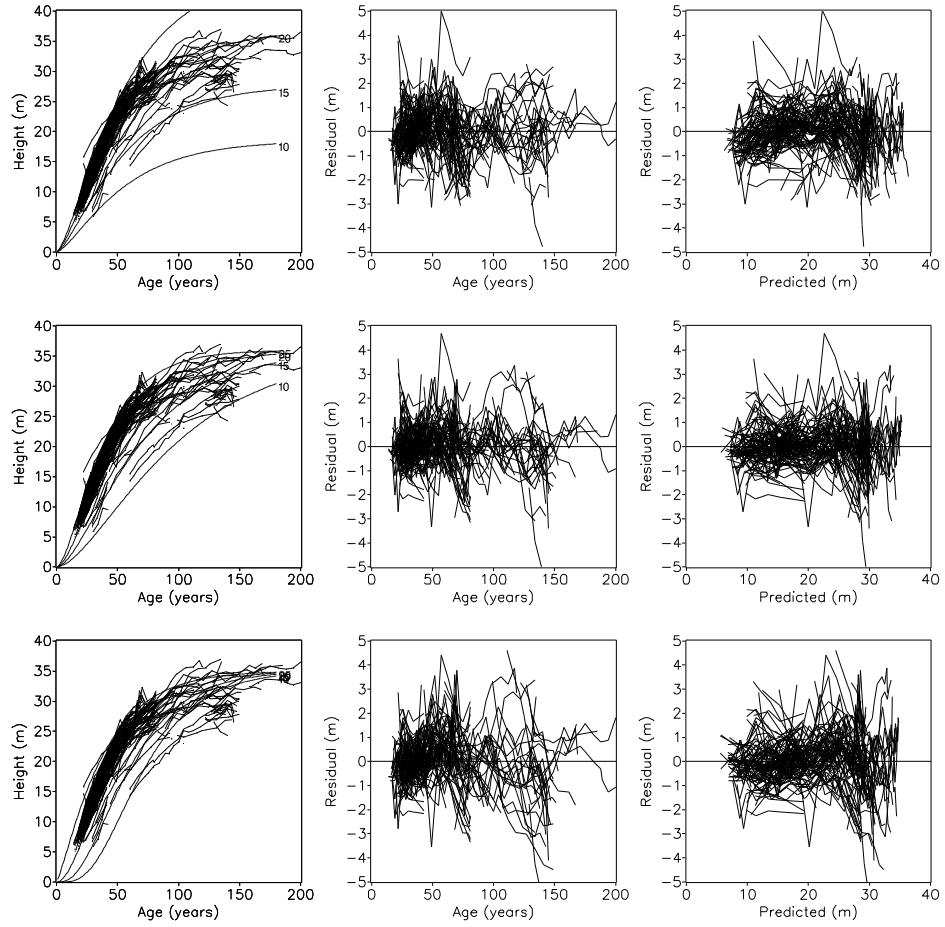


Figure I.1: Site index curves and residuals for the three forms of the Chapman-Richards equation, Equations (I.5), (I.7) and (I.8). Numbers refers to height at base age 50 years.

reference heights were only available for about one-third of the plots which resulted in the loss of about half of the observations of dominant height. This is especially evident from the lack of observations at old ages (>120 years).

The base-age invariant method produced only a small improvement in model fit (Table I.2) but provided a significant improvement to the distribution of residuals (Figure I.2 and I.3). More importantly, the base-age invariant method allowed the use of all data for fitting the equation, which made available twice as many observations from three times as many experiments. However, test statistics of the residuals revealed significant autocorrelation in the regression (Figure I.2, second row).

Inclusion of a first-order serial correlation regime removed all the serial correlation from the residuals (Figure I.2, third row). The final fit showed no obvious systematic biases or trends in residuals (Figure I.2, Table I.3) with respect to age, predicted height or predicted site index at a base age of 50 years (not shown). This corrected Equation (I.9) had the best fit of the many equations tested. Further, based on the position of the asymptote and inflection point, curve shapes produced by this final fit had desirable extrapolation properties (Figure I.3 and I.4).

Discussion

Site curves may be estimated in a number of different ways. The most common method is the difference equation method in which height at a given age is estimated using the height and age at the previous measurement as predictor variable (see Clutter et al., 1992). Curtis et al. (1974b) found that this method produces bias since the height is assumed with error when it occurs on the left-hand side of the site equation while assumed free of error when it occurs on the right-hand side of the equation. The implications of the bias may be ignored when the main purpose of the model is prediction and the expected error is similar in the data used for prediction as in the estimation dataset. However, when the parameter estimates themselves are important, i.e. in some biologically meaningful relationship measurement error models are appropriate. Borders et al. (1988) suggested the use of all possible differences for modelling basal area and volume growth. This method was used to estimate site index functions by Goelz and Burk (1992, 1996), who subsequently modelled the error structure and inflated the standard error of parameter estimates. This method is similar to major axis regression and geometric mean regression and appeared to recover the curve-shape well. However, Furnival et al. (1990) found that the different methods for fitting site curves are analytically identical, although their results only apply to models linear in the parameters. Recent research suggests that the all possible differences approach may also yield biased estimates (Dr.

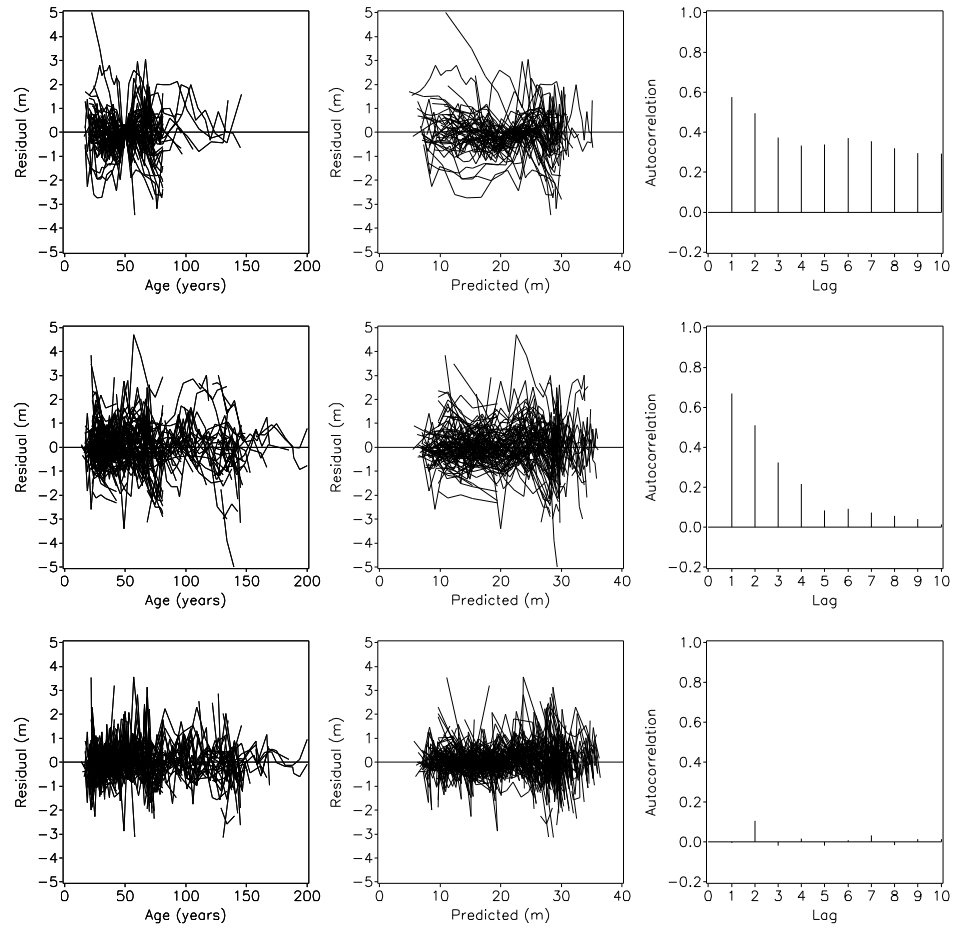


Figure I.2: Residuals and estimates of autocorrelation of Equation (I.9). First row is residuals and autocorrelation of the base-age specific site model. Second and third row is residuals and autocorrelation for the base-age invariant method.

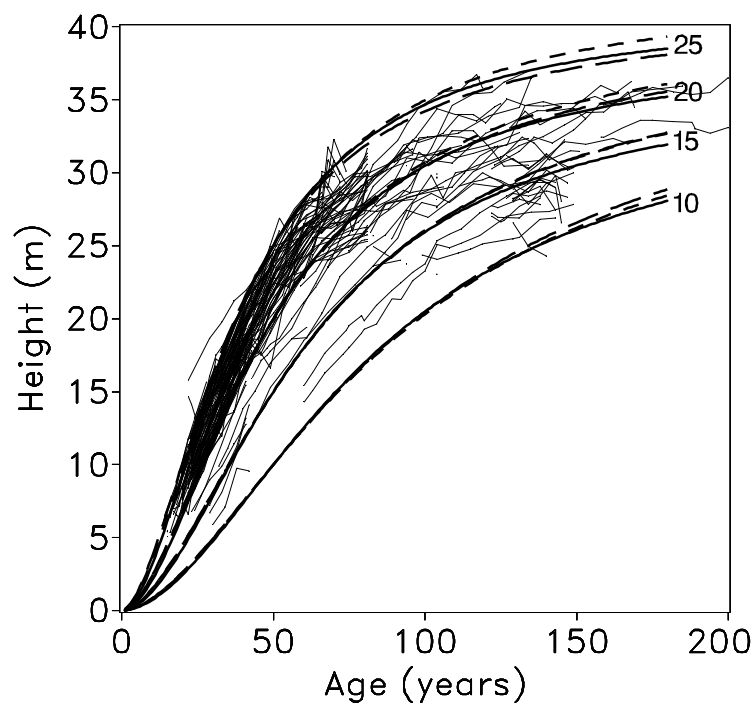


Figure I.3: Site index curves for the dynamic site equation based on Equation (I.9). ——— BS estimation, — — — BI estimation and - - - BI (AR1) estimation. Numbers refers to height at base age 50 years.

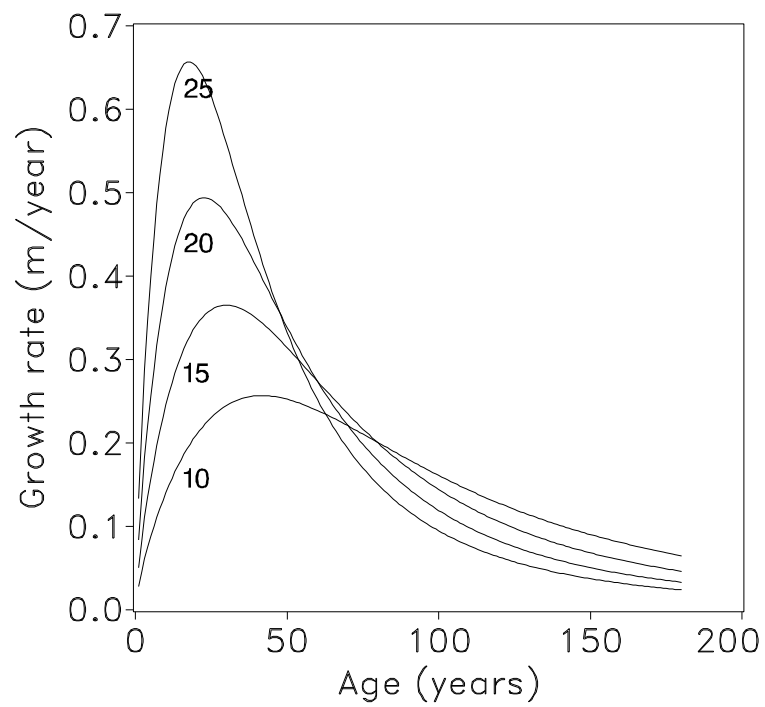


Figure I.4: Growth rates of the dynamic site equation based on Equation (I.9). Numbers refers to height at base age 50 years.

Table I.3: Lack of fit statistics for estimation of Equation (I.9). Root mean square error (RMSE), average bias and standard error of estimates (SEE) by height class (HC). BS and BI refer to base-age specific and base-age invariant estimation method, respectively and AR1 refers to the inclusion of a first order autocorrelation regime.

Method		BS				BI				BI (ARI)				
Class	Freq.	Bias	Bias	SEE	SEE	Freq.	Bias	Bias	SEE	SEE	Bias	Bias	SEE	SEE
		m	%	m	%		m	%	m	%		m	%	
All	855	-0.06	-0.3	0.92	4.6	1520	-0.00	0.0	0.96	4.6	0.00	0.0	0.76	3.7
<10	70	-0.09	-1.0	0.96	11.6	134	-0.20	-2.5	0.93	11.5	-0.18	-2.2	0.90	11.1
10.0-12.5	75	-0.02	-0.2	0.90	7.9	136	-0.12	-1.1	1.02	9.0	0.04	0.3	0.80	7.1
12.5-15.0	72	0.00	0.0	0.98	7.1	141	0.06	0.4	1.27	9.2	-0.04	-0.3	0.96	7.0
15.0-17.5	98	0.04	0.3	0.96	5.9	152	0.03	0.2	0.98	6.0	-0.01	0.1	0.77	4.7
17.5-20.0	101	-0.12	-0.6	0.83	4.4	141	-0.09	-0.5	1.00	5.3	-0.10	-0.5	0.75	4.0
20.0-22.5	91	-0.18	-0.9	0.75	3.5	122	-0.01	0.0	1.14	5.4	0.14	0.7	0.97	4.6
22.5-25.0	100	-0.12	-0.5	0.85	3.6	154	-0.10	-0.4	1.61	6.7	-0.08	-0.4	1.33	5.6
25.0-27.5	113	-0.34	-1.3	1.18	4.5	166	-0.27	-1.0	1.65	6.3	-0.11	-0.4	1.10	4.2
27.5-30.0	86	0.13	0.5	0.97	3.4	170	0.14	0.5	1.34	4.5	0.02	0.1	1.18	4.1
30.0-32.5	36	0.52	1.7	1.04	3.4	122	0.33	1.1	1.82	5.8	0.27	0.9	1.58	5.1
>32.5	13	0.24	0.7	-	-	82	0.47	1.4	3.09	9.0	0.27	0.8	2.21	6.4

C.J. Cieszewski, WSFR, The University of Georgia, Athens, GA, personal communication, June 2004). Further, the claimed base-age invariance of the estimation method and algebraic formulation used by Goelz and Burk (1992) and subsequent papers by Payandeh and Wang (1994); Wang and Payandeh (1994, 1995, 1996) was later refuted by Bailey and Cieszewski (2000).

In their original paper Bailey and Clutter (1974) suggested that the site-specific variable could be estimated individually for each site using nonlinear least squares. This approach uses only tenable statistical assumptions, since no reference heights subject to error enter into the right hand side of the site equation causing the parameter estimates to be biased. Using a similar approach Cieszewski (2003) estimated a base-age invariant site equation using a nonlinear mixed-effects model (`nlme`) in which the random site-specific effects were estimated simultaneously with the fixed effects. The advantage of this method is that the use of degrees of freedom is reduced considerably. However, `nlme` would usually assume that the random effect is normally or otherwise distributed and that the data available for estimation represents a random sample of the population, which is unlikely to be true as also noted by Cieszewski (2003). In this study I estimated the site-specific variable individually for each experiment, using indicator variables and hence made no assumptions on the underlying distribution of the random effect. Since the loss of degrees of freedom become less critical when the number of observations increase, using a fixed effects model may be less problematic in the case of the relatively large dataset used in this study.

No matter the method of estimation, the base-age invariant method evaded the need for prior information on site index. This allowed all of the data to be used in modelling the site equations regardless that the individual sample plots neither contained measurements at any base age common for all the sample plots nor did share the same range of ages. At a base age of 50 years, this allowed for the utilisation of twice the amount of observations of height and age from three times as many experiments.

Comparing the base-age specific and base-age invariant methodologies, the curve shapes produced by the two methods are very similar (Figure I.3). However, when introducing a first order autocorrelation regime a slight change in curve shapes is observed. Such change in curve shape should be carefully examined since introduction of autocorrelation may hide serious problems within the model or data. In particular, misspecification will lead to seeming autocorrelation. Thus, correcting the residuals in this case will hide the problem and lead to misinterpretation of the observed trends. A similar change in curve shape was observed by Cieszewski (2003). He was however able to correct for the problem by introducing second order autocorrelation. In the present study introduction of second order autocorrelation did not mitigate the problem, and a slight misspecification may be present in the model. However, since no apparent bias is observed in the residuals

of the model before correcting for autocorrelation (Figure I.2, second row) the problem may be quite small.

Conclusion

Based on the findings of this study, estimation of the base-age invariant form of the various equations used only tenable statistical assumptions and provided a significant improvement to the distribution of residuals. Further, the base-age invariant method evaded the need for prior information on site index and allowed for estimation without interpolation or extrapolation from the original data. The three base-age invariant site equations derived from the Chapman-Richards equation [Equations (I.5), (I.7) and (I.8)] did not have the flexibility and extrapolation properties desired for the site equation. Among the many base-age invariant equations that were tried in relation to this study, Equation (I.9) had a better or similar fit, was more parsimonious and had superior extrapolation properties.

Acknowledgements

I gratefully acknowledge the many constructive suggestions made by Vivian Kvist Johannsen, Henrik Meilby and Jens Peter Skovsgaard in relation to this study. Furthermore, I owe a dept of gratitude to Professor David W. Hann for his inspiration and Oregon State University for hosting me during the making of this study. The study was funded by Danish Forest & Landscape research Institute, Danish Forest and Nature Agency and Danish Agricultural and Veterinary Research Council.

Literature cited

- Amateis, R. L. and Burkhardt, H. E. (1985). Site index curves for loblolly pine plantations on cutover site-prepared lands. *South. J. Appl. For.*, 9:166–169.
- Bailey, R. L. and Cieszewski, C. J. (2000). Development of a well-behaved site-index equation: jack pine in north-central Ontario: comment. *Can. J. For. Res.*, 30:1667–1668.
- Bailey, R. L. and Clutter, J. L. (1974). Base-age invariant polymorphic site curves. *For. Sci.*, 20:155–159.
- Borders, B. E., Bailey, R. L., and Clutter, M. L. (1988). Forest growth models: Parameter estimation using real growth series. In Ek, A. R., Shifley, S. R., and Burk, T. E., editors, *Forest growth modelling and prediction*,

- Proc. IUFRO conf. Vol. 2. USDA For. Serv. Gen. Tech. Rep. NC-120, pages 660–667. 1152 p.
- Cao, Q. V. (1993). Estimating coefficients of base-age-invariant site index equations. *Can. J. For. Res.*, 23:2343–2347.
- Carbonnier, C. (1971). Bokens produktion i Södra Sverige. *Studia Forestalia Suecica*, 91:1–89.
- Carmean, W. H. (1956). Suggested modifications of the standard Douglas-fir site curves for certain soils in southwestern Washington. *For. Sci.*, 2:242–250.
- Cieszewski, C. J. (2001). Three methods of deriving advanced dynamic site equations demonstrated on inland Douglas-fir site curves. *Can. J. For. Res.*, 31:165–173.
- Cieszewski, C. J. (2003). Developing a well-behaved dynamic site equation using a modified Hossfeld IV function $y^3 = (ax^m)/(c+x^{m-1})$, a simplified mixed-model and scant subalpine fir data. *For. Sci.*, 49:539–554.
- Cieszewski, C. J. and Bailey, R. L. (2000). Generalized algebraic difference approach: theory based derivation of dynamic site equations with polymorphism and variable asymptotes. *For. Sci.*, 46:116–126.
- Clutter, J. L., Fortson, J. C., v. Pienaar, L., Brister, G. H., and Bailey, R. L. (1992). *Timber management - a quantitative approach*, pages 30–62. Krieger Publishing Compagny, Florida. 333 p.
- Curtis, R. O. (1964). A stem-analysis approach to site-index curves. *For. Sci.*, 10:241–256.
- Curtis, R. O., DeMars, D. J., and Herman, F. R. (1974a). Which dependent variable in site index-height-age regressions? *For. Sci.*, 20:74–87.
- Curtis, R. O., Herman, F. R., and DeMars, D. J. (1974b). Height growth and site index for Douglas-fir in high-elevation forests of the Oregon-Washington Cascades. *For. Sci.*, 20:307–316.
- Dent, J. B. and Blackie, M. J. (1979). *Systems Simulation in Agriculture*, pages 94–117. Applied Science Publishers ltd., London. 180 p.
- Eichhorn, F. (1904). Beziehungen zwischen Bestandeshöhe und Bestandesmasse. *Allg. Forst. Jagdztg.*, 80:45–49.
- Frothingham, E. (1918). Height growth as a key to site. *J. For.*, 16:754–760.
- Frothingham, E. (1921). Classifying forest sites by height growth. *J. For.*, 19:1–14.

-
- Furnival, G. M., Gregoire, T. G., and Valentine, H. T. (1990). An analysis of three methods for fitting site-index curves. *For. Sci.*, 36:464–469.
- Goelz, J. C. G. and Burk, T. E. (1992). Development of a well-behaved site index equation: jack pine in north central Ontario. *Can. J. For. Res.*, 22:776–784.
- Goelz, J. C. G. and Burk, T. E. (1996). Measurement error causes bias in site index equations. *Can. J. For. Res.*, 26:1585–1593.
- Gram, J. P. (1879). Om Konstruktion af Normal-Tilvækstoversigter, med særligt Hensyn til Iagttagelserne fra Odsherred. *Tidsskrift for Skovbrug*, 3:207–270. Denmark.
- Gyldenfeldt, W. (1881). En Lokal Tilvæxtoversigt for Bøg. *Tidsskrift for Skovbrug*, 5:269–284.
- Henriksen, H. A. and Bryndum, H. (1996). Bøgeforyngelser i Stagsrode Skov. In Skovsgaard, J. P. and Morsing, M., editors, *Bøgeselvforryngelser i Østjylland*, The Research Series no. 13, pages 5–162. Danish Forest and Landscape Research Institute, Denmark. 215 p.
- Holm, O. G. T. (1892). Tilvækstoversigt for Bøgehøjsskov paa Grevskabet Langelands Distrikt. *Tidsskrift for Skovvæsen*, 4:177–180.
- Holten, A. (1894). Tilvækstoversigt for Bøgehøjsskov i Fløjstrup Skov under Baroniet Vilhelmsborg. *Tidsskrift for Skovvæsen*, 6:43–47.
- Johannsen, V. K. (2002). Selection of diameter-height curves for even-aged oak stands in Denmark. Dynamic growth models for Danish forest tree species, Working paper 16, Danish Forest and Landscape Research Institute, Hørsholm, Denmark. 70 p.
- Larsen, P. H. and Johannsen, V. K. (2002). *Skove og Plantager 2000*. Statistics Denmark, Centre for Forest, Landscape and Planning, Danish Forest and Nature Agency, Denmark. 171 p.
- Lenhart, J. D., Hunt, E. V., and Blackard, J. A. (1986). Site index equations for loblolly and slash pine plantations on non-old-fields in east Texas. *South. J. Appl. For.*, 10:109–112.
- Meyer, H. (1940). A mathematical expression for height curves. *J. For.*, 38:415–420.
- Møller, C. M. (1933). Boniteringstabeller og Bonitetsvise Tilvækstoversigter for Bøg, Eg og rødgran i Danmark. *Dansk Skovforenings Tidsskrift*, 18:537–623.

- Monserud, R. A. (1984). Height growth and site-index curves for inland Douglas-fir based on stem analysis data and forest habitat type. *For. Sci.*, 30:943–965.
- Näslund, M. (1936). Skogsforsöksastaltens gallringsforsök i tallskog. *Meddelanden från Statens Skogsforsöksanstalt*, 29:1–169.
- Oppermann, A. (1914). God dansk Bøgeskov, belyst ved tre Tilvækstoversigter. *Det Forstlige Forsøgsvæsen*, 4:341–377.
- Parker, H. (1942). Dominant height and average diameter as a measure of site quality. *For. Chron.*, 18:152–156.
- Payandeh, B. and Wang, Y. (1994). Relative accuracy of a new base-age invariant site index model. *For. Sci.*, 40:341–348.
- Pienaar, L. V. and Shiver, B. D. (1980). Dominant height growth and site index curves for loblolly pine plantations in the Carolina Flatwoods. *South. J. Appl. For.*, 4:54–59.
- Richards, F. J. (1959). A flexible growth equation for empirical use. *Journal of Experimental Botany*, 10:290–300.
- Schober, R. (1972). *Die Rotbuche 1971*. Saurländer's Verlag, Hannover, Germany. 333 p.
- Stuhr, G. (1978). Über das Wachstum von Buchenbeständen in Schleswig-Holstein. *Forstarchiv*, 49:256–259.
- Wang, Y. and Payandeh, B. (1994). Application of the Kalman filter model in site index equation construction. *Can. J. For. Res.*, 24:1415–1418.
- Wang, Y. and Payandeh, B. (1995). A base-age invariant site index model for aspen stands in north central Ontario. *For. Ecol. Man.*, 72:207–211.
- Wang, Y. and Payandeh, B. (1996). Evaluating a dimensionally compatible height growth modelling approach. *For. Chron.*, 72:647–650.

Paper II

A state-space approach to stand growth modelling

A state-space approach to stand growth modelling of European beech

Thomas Nord-Larsen ^{*1} and Vivian Kvist Johannsen ^{*2}

^{*}Royal Veterinary and Agricultural University
Forest & Landscape
Hørsholm Kongevej 11, DK-2970 Hørsholm, Denmark

Abstract

Static models of forest growth, such as yield tables or closed-form mathematical models, fail to recognise that forest stands are dynamic systems, subject to sudden changes caused by silvicultural interventions. Based on permanent sample plot data, covering a wide range of initial spacings and thinning practises, we developed a dynamic stand growth model of European beech in Denmark. The model entailed three equations for predicting dominant height growth, basal area growth, and mortality.

The signs of the parameter estimates generally confirmed the anticipated growth paths of dominant height and basal area. Although statistical tests indicated significant systematic deviations between observed and predicted values, the deviations were small and of little practical importance. Cross evaluation procedures indicated that the model may be applied across a wide range of growth conditions and thinning practises in Denmark without significant loss of precision.

Keywords: difference equation, dominant height, basal area, stem number, *Fagus sylvatica* L.

Introduction

Fitting of simple growth curves for prediction of stand level variables such as average height, stand basal area or stem number is an old discipline in forest growth modelling (e.g. Borders and Bailey, 1986; Clutter, 1963; Gram, 1879; MacKinney and Chaiken, 1939). Such models describe the course of stand variables over time and may yield reasonable estimates in many situations. However, the static models fail to recognise that forest stands are dynamic systems, subject to sudden changes caused by silvicultural interventions. As the intensity of management increases, interventions may vary in timing and intensity and the stand variables may follow a potentially infinite number of paths (García, 1994).

¹Corresponding author. E-mail: tnl@kvl.dk, Phone: (+45) 35281758, Fax: (+45) 35271517

²E-mail: vkj@kvl.dk, Phone: (+45) 35281699, Fax: (+45) 35271517

The state-space approach relies on the assumption that the state of a system at any given time contains the information needed to predict the behaviour of the system in the future (García, 1994). Hence, the state of a system may be viewed as the cumulated information of the past, and no further information of the past is needed to predict the future behaviour of the system. The state-space approach is adequate for modelling subjects that undergo sudden changes because explicit modelling of the complex relation between interventions and responses of the system is avoided. Instead, change (increment or change in stem numbers) is modelled from the state of the system at any point in time and any future state is predicted from the current state and current and future actions through iteration.

Covering 17% of the total forest area European beech is the most common deciduous species in Denmark (Larsen and Johannsen, 2002) and also the most significant in economic terms. Current models for predicting stand level growth of beech in Denmark are standard yield tables based on graphical smoothing of permanent sample plot data (Møller, 1933; Henriksen and Bryndum, 1996). Despite the practical importance of these tables, the methods applied in their making have generally lacked statistical rigour and objectivity. The aim of this study was to develop stand level models for predicting the growth of even-aged stands of European beech in Denmark. Based on the previous discussion the main focus was the development of dynamic models based on a state-space approach.

Materials

The gross data for developing stand level models for beech comprised 60 permanent, even-aged and mono-specific spacing, species and thinning experiments in beech and a total of 146 individual plots. Plot sizes varied between 0.07 and 2.65 ha with an average of 0.40 ha. The experiments were located in most parts of Denmark and cover a wide range of different site types and growth conditions. The data were collected during the years from 1872 to 2004 and the stands were observed for 10 to 120 years. The number of measurement occasions totaled 1484.

The data included a wide range of different treatments in terms of initial spacing and thinning intensities from unthinned controls to heavily thinned ones. In the thinning experiments, the treatments included A-, B-, C-, and D-grade thinnings. Usually, the D-grade is thinned to a basal area of 50% relative to the unthinned control (A-grade). The B- and C-grades are intermediate, dividing the interval between A- and D-grades equally. Some plots were managed according to other thinning strategies, such as group- or selection-thinning and others were managed according to the thinning strategy typical at the time.

In the majority of the sample plots, all trees were numbered, marked

permanently at breast height (1.3 m) and recorded individually. In 451 measurements carried out before 1930 and in some very young stands with high stem numbers, trees were recorded in tally lists to 1-cm diameter classes (or 1-inch classes before 1901). Also in 13 very young stands with high stem numbers, only a subset of stems were measured, e.g. every fifth or tenth row. Breast height diameters were obtained by averaging two perpendicular calliper readings. Observations also included records on whether the tree was alive or dead at the time of measurement. Heights were typically measured on about 30 trees per plot. Finally, soil texture analyses were carried out in 48 experiments, providing information on percentages of clay, silt, fine sand and coarse sand in the top one metre of the mineral soil.

Based on paired observations of diameter and height, height-diameter equations were estimated for each plot and measurement combination using a modified Näslund-equation (Näslund, 1936; Johannsen, 2002):

$$h = 1.3 + \left(\frac{d}{\alpha + \beta \cdot d} \right)^3 \quad (\text{II.1})$$

where d is diameter at breast height, h is total tree height and α and β are parameters to be estimated. The equations were used to estimate the height of trees not measured. Dominant height, defined as mean height of the 100 thickest trees per hectare, H_{100} (m), was subsequently calculated for each plot and measurement combination. In the few cases where stem numbers were less than 100 per hectare, H_{100} was estimated as the mean height.

Stem numbers, N (1000 ha⁻¹), were calculated as the number of individual trees per hectare taller than 1.3 m. When trees forked below 1.3 m, each stem was measured individually but multiple stems from the same root were counted as one tree. Within the research plots, trees were typically separated into over- and understorey and the understorey was measured less intensively than the overstorey. Understorey trees were excluded from this analysis.

Stand basal area, G (m² ha⁻¹), of each plot was estimated by summation of individual tree basal areas calculated from the diameter measurements. When trees were recorded in tally lists, the middiameter of each class was used as an estimate of the diameter of all trees in that class. Diameter of the mean basal area tree, D_g (cm), was derived from the estimates of N and G . The data represent a wide range of stand-ages and stand values such as H_{100} , G , D_g and N (Table II.1, Figure II.1).

Methods

Any number of stand variables may be chosen to describe stand-level growth and the choice depends on the desired level of resolution and the practical

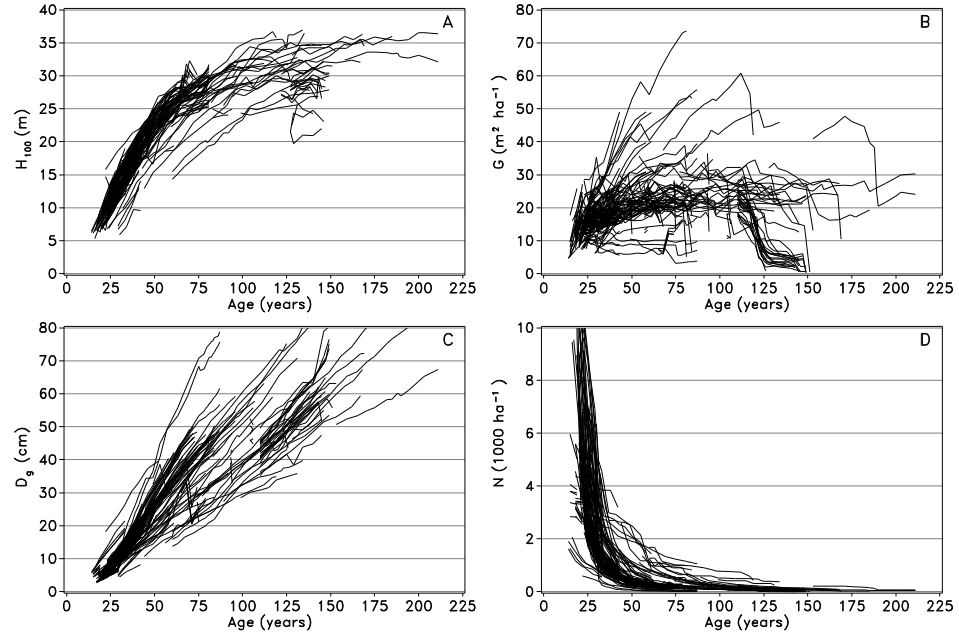


Figure II.1: Stand-level values of H_{100} (A), G (B), D_g (C) and N (D).

Table II.1: Summary statistics of dominant height (H_{100}), basal area (G), stem number (N), quadratic mean diameter (D_g) and age (T).

Variable	Unit	N	Mean	Minimum	Maximum	Std. Dev.
H_{100}	m	1458	20.88	5.08	36.95	7.69
G	$\text{m}^2 \text{ha}^{-1}$	1458	20.04	0.21	73.58	8.92
N	ha^{-1}	1458	1372	0.49	24720	2317
D_g	cm	1458	26.72	2.70	82.85	17.56
T	years	1458	60.70	14	200	47.65

application. Among the most commonly used variables in stand level models are dominant height (H_{100}), stand basal area (G), stem number (N), diameter of the mean basal area tree (D_g) and stand volume (V) and their derivatives. Since D_g and V may be derived from the first three variables, we modelled H_{100} , G and N in this study.

Model description

The model form used to describe the development of different variables essentially depends on the modelling subject and a great variety of model forms have been presented for various forestry applications. The growth paths of H_{100} and G essentially results from two competing effects: an intrinsic tendency toward unlimited growth and restraints imposed by environmental factors (competition for limited resources). The two effects may be synthesized into two basic laws:

1. Growth is fundamentally multiplicative.
2. Relative growth is always decreasing.

The resulting curve is often described as a sigmoid form with an initial expansion followed by a dampening effect. Among the most well known models are the Gompertz (Gompertz, 1832), logistic (Verhulst, 1845, 1847), monomolecular (Mitscherlich, 1919), Bertalanffy (1957) and Chapman-Richards (Richards, 1959) equations. Despite the apparent diversity of growth models, Zeide (1993) found that most of the mentioned equations can be transformed into a single equation in which the two opposing factors, initial multiplicative expansion followed by exponential dampening are expressed as:

$$\frac{dy}{dt} = \alpha y^\beta e^{\gamma y} \quad (\text{II.2})$$

where y represents the size of the modelling subject and α , β , and γ are parameters. This equation was initially developed for predicting individual tree growth and has in a number of studies been expanded to include a number of additional elements such as basal area and basal area in larger trees (Hann and Hanus, 2002a,b; Johannsen, 1999). Different forms of equation (II.2) have also been used in stand growth modelling (Johannsen, 1999). Greatly inspired by the latter work and based on the proposition that density measured as stand basal area affects both basal area growth and dominant height growth, we used the following equations to describe height and basal area growth:

$$\frac{dH_{100}}{dt} = \alpha_1 H_{100}^{\alpha_2} e^{\alpha_3 H_{100} + \alpha_4 G} \quad (\text{II.3})$$

$$\frac{dG}{dt} = \beta_1 G^{\beta_2} e^{\beta_3 G + \beta_4 H_{100}^{\beta_5}} + FV[G] \quad (\text{II.4})$$

where $FV[G]$ (Forcing Value) is shifts in G caused by thinnings and $\alpha_1 - \alpha_4$ and $\beta_1 - \beta_5$ are parameters to be estimated.

The reduction in stem number in even-aged stands is caused by thinning operations and mortality. When using the state-space approach, thinnings are simulated explicitly and need not be modelled. Mortality may be perceived to consist of two factors: i) simple chance of death and ii) a density-dependent mortality that increases with density. We modelled the simple chance of death as a fraction of the stem number and the density dependent reduction in stem-numbers by the exponential of the inverse relative spacing ($RS = \sqrt{10000/N/H}$):

$$\frac{dN}{dt} = \gamma_1 N^{\gamma_2} e^{\gamma_3 \sqrt{N} H_{100}} + FV[N] \quad (\text{II.5})$$

where $FV[N]$ denotes shifts in N caused by thinning and $\gamma_1 - \gamma_3$ are parameters to be estimated. Preliminary estimation of the model revealed that a simpler model and similar fit statistics were obtained for $\gamma_2=1$, while ensuring a reasonable model behaviour. Thus in the final estimation of the system of equations, γ_2 was fixed at 1.

In equation (II.3), (II.4) and (II.5) the state-space problem is formulated as a continuous-time model. However, this may be conceptually wrong since trees in fact have distinct periods of change. Further, since the equations above have no closed form solution they must be estimated numerically which is rather cumbersome. To reduce the computational load we used a discrete-time model in which $\Delta x/\Delta t$ is substituted for dx/dt :

$$\frac{\Delta H_{100}}{\Delta t} = \alpha_1 H_{100}^{\alpha_2} e^{\alpha_3 H_{100} + \alpha_4 G} \quad (\text{II.6})$$

$$\frac{\Delta G}{\Delta t} = \beta_1 G^{\beta_2} e^{\beta_3 G + \beta_4 H_{100}^{\beta_5}} + FV[G] \quad (\text{II.7})$$

$$\frac{\Delta N}{\Delta t} = \gamma_1 N^{\gamma_2} e^{\gamma_3 \sqrt{N} H_{100}} + FV[N] \quad (\text{II.8})$$

Site-specific effects

Modelling growth and yield requires some measure of site quality to make reasonable forecasts. In a number of studies the site-specific effects have

been included by allowing some parameters to be local or plot-specific and others to be general or global (Bailey and Clutter, 1974; García, 1983; Cieszewski and Bailey, 2000). Subsequently the local parameters may be related to site-index or environmental properties such as climate, elevation or soil properties or the parameter estimate may be perceived as an indicator of site quality itself (McDill and Amateis, 1992; Johannsen, 1999; Leary et al., 1997).

Which parameter to make local and which to make global depends on the modelling subject. The simplest formulation of equation (II.6) and (II.7) emerges from leaving α_1 and β_1 to be local and the remaining parameters to be global since the site-specific parameter is then a simple factor. Preliminary studies showed similar fit statistics and extrapolation properties of making α_1 and α_2 local whereas making α_3 local resulted in worse estimates. Although the fit statistics showed no differences between the two first formulations, making α_1 and β_1 local resulted in greater ease of fit and a more parsimonious model.

When fitting a similar system of equations Johannsen (1999) hypothesized that it is possible to find an allometric relation between the growth rates of both height and basal area. Hence the site-specific effect of both equations may be captured in one rate constant (α_1). Preliminary studies showed that α_1 and β_1 were highly correlated and their relation was adequately modelled by a linear model:

$$\begin{aligned}\frac{\Delta H_{100}}{\Delta t} &= \alpha_1 H_{100}^{\alpha_2} e^{\alpha_3 H_{100} + \alpha_4 G} \\ \frac{\Delta G}{\Delta t} &= (\beta_{01} + \alpha_1 \cdot \beta_{02}) G^{\beta_2} e^{\beta_3 G + \beta_4 H_{100}^{\beta_5}} + FV[G] \\ \frac{\Delta N}{\Delta t} &= \gamma_1 N^{\gamma_2} e^{\gamma_3 \sqrt{N} H_{100}} + FV[N]\end{aligned}\tag{II.9}$$

where the local parameter β_1 is substituted by a function of α_1 , that is estimated locally, and the two global parameters β_{01} and β_{02} . The remaining parameters are estimated globally.

Model estimation

Different forms of the state-space approach have been used by various authors to model individual tree or stand-level growth. García (1983) modelled height growth of even-aged stands by a stochastic differential equation. The parameters were estimated simultaneously by a maximum-likelihood procedure that included an explicit expression of the error term.

Instead of using continuous-time models, a number of authors have fitted discrete-time models of individual tree and stand level growth. Lynch and

Moser Jr. (1986) related average rates of change to the current state of the system ("averaging method" or "difference quotient method"). Clutter (1963) recognised that the average growth rate is more likely to be closest to the actual growth rate at the midpoint of the measurement interval and related average changes to the interpolated state variables at the midpoint of the observed growth interval ("midpoint method").

Rather than assuming the growth rate to be constant and equal to average growth throughout the growth period McDill and Amateis (1993) suggested that discrete time models should be fitted from observations with any time interval using the hypothesized functional form of the difference equation as basis for interpolation. Such approach was later generalised for predicting annual growth rates for a number of individual tree and stand level variables (Cao, 2000, 2004; Johannsen, 1999).

Following the approach of McDill and Amateis (1993) the estimation problem may be written as a series of annual difference equations that increment growth from some initial state to the state at some point in time, using the years between the two observations as the number of iterations. Consider height increment, equation (II.6) may be written as:

$$\hat{H}_{i,t+1} = H_{i,t} + f(H_{i,t}, G_{i,t}) + \varepsilon_{i,t+1} \quad (\text{II.10.1})$$

$$\hat{H}_{i,t+2} = \hat{H}_{i,t+1} + f(\hat{H}_{i,t+1}, \hat{G}_{i,t+1}) + \varepsilon_{i,t+2} \quad (\text{II.10.2})$$

$$\vdots$$

$$\hat{H}_{i,t+j} = \hat{H}_{i,t+j-1} + f(\hat{H}_{i,t+j-1}, \hat{G}_{i,t+j-1}) + \varepsilon_{i,t+j} \quad (\text{II.10.j})$$

where $f(H_{i,t}, G_{i,t})$ is expressed in equation (II.9) and models annual height increment at the i th plot at the time $t + j$ ($j = 0, 1, 2, \dots, n$). The parameters of the annual difference equation may be estimated using a nonlinear least squares procedure that minimizes the squared deviations of $\hat{H}_{i,t+j}$ from $H_{i,t+j}$.

As indicated in equation (II.10.1), the procedure requires some initial observation to initiate the iterations. The initial state may be either (Johannsen, 1999):

1. Fixed initial values
2. The first measurement at each plot
3. The previous measurement of each state-variable (also known as "the short shooting method")
4. Estimated initial values i) common to all observations, ii) common to each plot or iii) unique for each observation.

Using fixed initial values for the estimation procedure as in (1) and (4) requires that all thinnings throughout the stands life have been recorded to account for shifts in G and N (see equation (II.7) and (II.8)). Since unrecorded thinnings oftentimes occurred before the establishment of the experiments, this option is precluded. Options (2) and (3) both use measured values as initial conditions and avoid the problem of silvicultural activities before the initiation of the experiments. Using the previous measurement as initial state prevents error accumulation due to errors in the shift vectors and this method to a greater extent reflects the practical application. Thus, the estimation procedure was carried out using option (3).

The system of equations presented in (II.9) is referred to as a seemingly unrelated regression (SUR) system since only one dependent variable occurs in each equation. If no error correlation exists between the individual regressions they may be treated as independent problems. However, if error correlations are present OLS estimates are inefficient. In this study cross-equation error correlations were included in a generalised least squares procedure using iterated seemingly unrelated estimation (ITSUR) (SAS Institute Inc., 1993).

The data used for this study represent a structure of repeated measurements on individual plots. Failure to recognize that within-plot measurements are correlated may result in inefficient estimates and underestimated standard errors when correlations are strong. When growth is viewed as an incremental process where only current conditions influence current growth, the problems of serial correlation are usually avoided (García, 1983; Seber and Wild, 1989). However, we explicitly modelled the serial correlation by including a generalised formulation of the first-order autoregressive model that accommodates the irregular spacing of measurements:

$$\varepsilon_i = \rho_m^{t_i - t_{i-1}} \varepsilon_{i-1} + u_i \quad (i = 1, 2, \dots), \quad (\text{II.11})$$

where ε_i is the error at the i th measurement, t is the time, ρ_m is the coefficient of correlation of the m th equation and the u_i 's are normally and independently distributed random errors.

Statistical fit of the model

Characterisation and assessment of errors cannot be performed directly on the model subject since the model predicts annual increment, which is not observed directly. Instead model evaluation may be carried out on the predicted state of the model subject at the end of the period. However, this leads to highly inflated estimates of fit statistics since much of the variation is explained by the initial state of the model subject. Instead the errors may be characterized by the deviations between predicted and observed periodic annual increment (*PAI*). The two measures were both applied in the analyses.

Model error were first characterised in terms of magnitude and distribution by plotting residuals against predicted values of the model subject. Further, residuals were plotted against observed values of other stand variables to expose any obvious trends. Temporal and regional trends were evaluated by plots of residuals against measurement years and natural-geographical regions according to Jakobsen (1976).

In addition to the visual appraisal of the errors a number of summary statistics were calculated for the entire data set as well as for different strata and initial values of the model subject. The summary statistics include average bias (AB), average absolute bias (AAB) and root mean squared error (RMSE).

Statistical tests for appraisal of accuracy, precision and stability of the model as well as the patterns and distribution of the residuals were carried out. The statistical tests of model bias included simultaneous F -tests for unit slope and zero intercept of the linear regression of observed versus predicted data (Dent and Blackie, 1979).

Tests of precision included R^2 -statistics and critical error confidence bounds (CEB) (Freese, 1960; Reynolds, 1984). Predictive performance and stability of the parameter estimates were evaluated by leave-one-out cross validation in which entire experiments were left out of the estimation data one at a time and subsequently the estimated model was applied to the left-out experiment. This procedure was extended to evaluate the stability of parameter estimates across site index, thinning intensities, regions and time of birth by iteratively leaving out different strata of data.

Results

Parameter estimates of the system of equations (II.9) were all significant ($P < 0.05$) except for β_{01} that was eliminated from the model. After reduction of the model all parameters were significant. The correlation coefficient of the height model (ρ_H) was non-significant, indicating no correlation of height growth in subsequent growth periods. The correlation coefficient of basal area growth (ρ_G) was highly significant, which may indicate that basal area growth in subsequent periods was positively correlated or may originate from any model misspecification.

The reduced model system accounted for more than 98% of the observed variation of H_{100} , G and N at the end of the growth period (Table II.2). Based on PAI the height and basal area models explained 35% and 77% of the total variation in annual growth, respectively, whereas the mortality model explained 31% of the observed annual changes in stem numbers.

Plots of residual PAI of H_{100} , G , N and D_g against their corresponding predicted values revealed no obvious trends (Figure II.2). Neither did plots of residual PAI for the three models against other stand variables

Table II.2: Parameter estimates of the system of equations presented in equation (II.9) along with their standard errors, t-values and significance levels. Average absolute bias (AAB), root mean square error (RMSE) and R^2 is calculated from the deviations between predicted and observed values at the end of the growth periods.

Model	Parameter	Estimate	Std. error	t-value	AAB	RMSE	R^2
H_{100}	α_1	0.0281 ^a	0.0100 ^a	2.80 ^a	0.4973	0.6947	0.9908
	α_2	1.9645	0.1972	9.96			
	α_3	-0.1838	0.0119	-15.43			
	α_4	0.0140	0.0022	6.24			
	ρ_H	0.0121	0.2359	0.05			
G	β_{02}	20.8794	7.6435	2.73	0.5781	0.8138	0.9914
	β_2	0.5693	0.0682	8.34			
	β_3	-0.0146	0.0028	-5.19			
	β_4	-0.0184	0.0066	-2.77			
	β_5	1.3004	0.0963	-13.50			
N	ρ_G	0.6009	0.0275	21.83	0.6100	1.9548	0.9882
	γ_1	0.0007	0.0001	5.37			
	γ_2	1.					
	γ_3	0.0343	0.0016	22.02			

^aEstimated individually for each experiment, number represents a simple average.

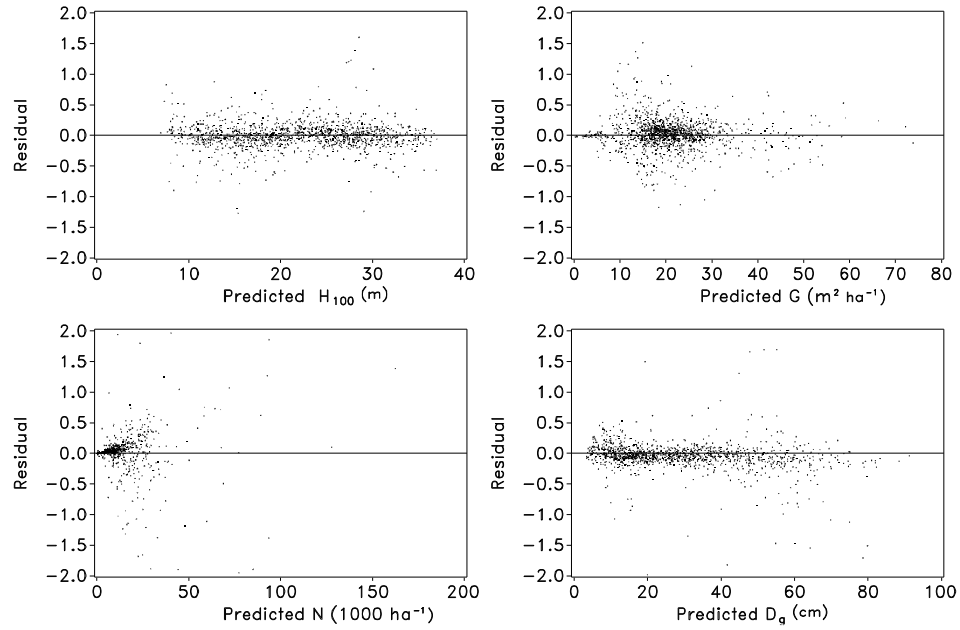


Figure II.2: Residual plots of H_{100} , G , N and D_g . Residuals are calculated as the difference between predicted and observed periodic annual increments. Residuals of D_g are derived from the estimates of G and N .

(not shown). Simultaneous F-tests confirmed that the height and mortality models were unbiased but showed a significant bias of the basal area model. However, the systematic deviations were small and of little practical importance.

Residuals were approximately homogeneous with zero mean for all three variables. Distributions of the residuals of the three models all deviated significantly from normality, although a graphical analysis indicated that deviations were small. Residuals of individual experiments had no significant serial correlation.

The cross-validation procedure of leaving out entire experiments in the estimation resulted in only a small increase in RMSE of the H_{100} and G models (0.6% and 5.4% respectively) but a rather large increase for the N model (61%). Further cross evaluation procedures in which different classes of data of data was left out based on different characteristics (i.e. site index, growth region, year of birth and thinning intensity) resulted in only a small increase in RMSE, indicating a remarkable stability of the parameter estimates.

Discussion

The signs of the parameter estimates generally confirmed the anticipated growth paths of both H_{100} and G (Table II.2). The positive α_2 and β_2 indicates an initial multiplicative expansion of growth followed by an exponential dampening as a result of the negative estimates of α_3 and β_3 . The estimate of α_4 indicates a positive response of dominant height growth for increasing levels of stand density (Figure II.3). This indicates an allometric response toward allocating more resources to height growth in crowded populations whereas in less crowded populations resources may be used for expansion of the crown or supporting structural components (i.e. stem and roots). The negative parameter estimate of β_4 and positive estimate of β_5 causes basal area growth to decrease as height increases (Figure II.3). As height may be viewed as an expression of physiological age, this may be an anticipated effect of aging, but may also reflect a tendency towards allocating more resources to the upper part of the stem and the crown as tree size increases in closed stands. The parameters of the mortality model show a limited chance of death that is increasing with increasing density.

Height and basal area growth peak at 10.7 m and 38.9 m² ha⁻¹, respectively, regardless of site quality, basal area, or height. This property of the selected models may be dubious from a biological point of view as we might expect the location of the peak to depend on e.g. site quality. We tested this proposition by modelling α_3 and β_3 as linear functions of the site-specific parameter, basal area (height model) and height (basal area model). In all cases the slope parameter was non-significant; hence the hypothesis of the location of peak growth varying with site quality, stand density, or height was not supported.

The effects of thinnings were modelled solely through the effect of the reduction in stemnumbers and basal area. Release effects were not modelled explicitly, although such effects have been observed for beech (Wiedemann, 1932). We attempted to model release effects by an exponentially decreasing multiplier function of the proportion of basal area removed in the thinning and the time since thinning. Although parameter estimates were significant, the predicted release effect on basal area growth was only present the first year after thinning and was very small. As the inclusion of release effects added to model complexity with little improvement to the model we did not include this in the final model.

The stability of the parameter estimates and fit statistics shown by the cross validation procedures indicated that the model may be applied across a wide range of growth conditions and thinning practises in Denmark without significant loss of precision. As suggested by a number of authors, growth of European forests may have changed significantly over the past century (Skovsgaard and Henriksen, 1996; Spiecker et al., 1996). This may have serious implications for the practical application of the estimated models to

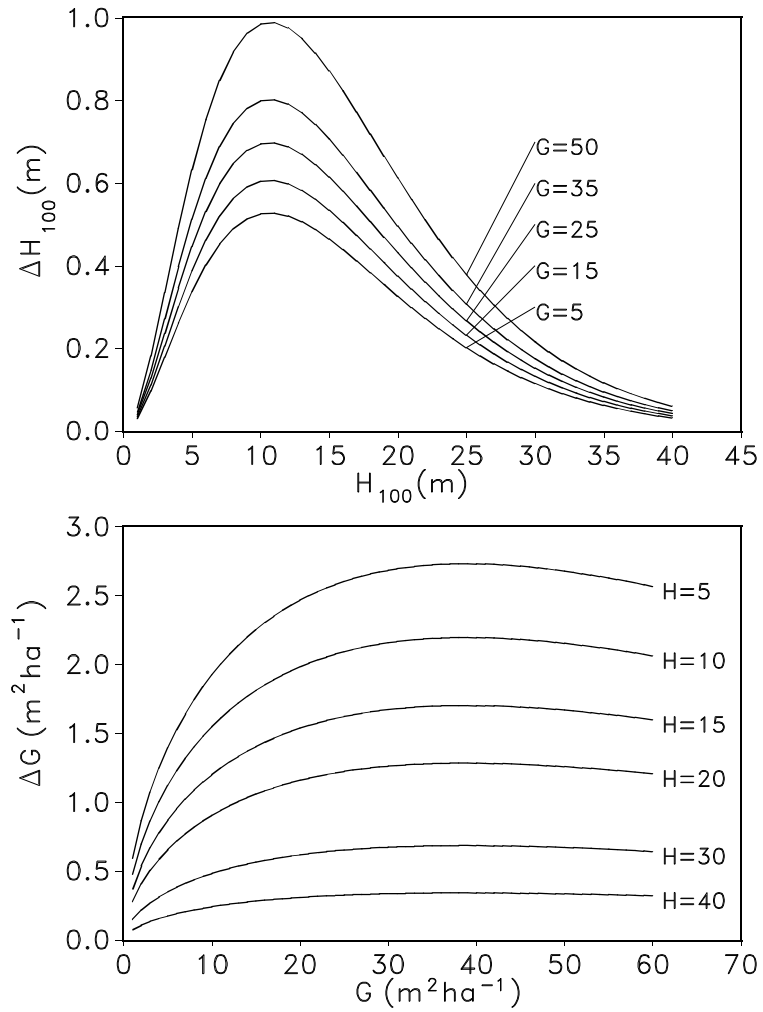


Figure II.3: Simulated annual height (H_{100}) and basal area (G) growth at different levels of basal area and height respectively.

predict future tree growth since parameters are estimated from data that dates back more than a century. Therefore, in a cross validation procedure parameters of the growth models were estimated on data from stands born before 1870 and applied to stands born after 1950 and vice versa. The results did not reveal any significant biases to suggest that future applications are affected by the change in forest growth.

The model was compared to the two most commonly used yield tables for beech in Danish forestry (Møller, 1933; Henriksen and Bryndum, 1996) by simulating height development of each of the height classes (Figure II.4). Simulations were carried out by first estimating the local parameter corresponding to each site class using all growth intervals. Subsequently, height growth was simulated from the first observation using the thinnings prescribed in the yield table. The height growth predicted by the dynamic model is greater than that of the yield table by Møller (1933). This tendency increases with age and decreasing site quality and is consistent with a later revision of the yield table (Møller and Nielsen, 1953). When comparing simulated growth with that of the yield table by Henriksen and Bryndum (1996) the results are much more consistent, although there is a tendency for the dynamic model to predict a more rapid height growth at young ages.

The site-specific parameter, α_1 , may be interpreted as a measure of site quality. For practical application of the stand model, α_1 must be estimated from observations of height and basal area. When the model is applied where beech has not been grown before or when there are no observations of stand variables the estimation cannot be carried out. We therefore related α_1 to the proportion of different soil fractions (clay, silt, fine sand, and coarse sand) in the uppermost 1 m of the soil to see if α_1 could be estimated from soil properties alone, but found no significant correlations. However, α_1 was highly correlated with the more traditional measure of site quality, site index (Figure II.5). Based on linear regression the site-specific parameter may be estimated from site index (dominant height at age 50) as $\alpha_1 = 0.000596 + 0.001378 \cdot SI$ ($R^2=0.56$).

There is often a limited amount of data available for estimating the site-specific parameter. We employed a sensitivity analysis to assess the importance of the available amount of data for estimating α_1 . First, plots having six or more measurements were selected. From this data set the first 1, 2, ..., 6 observations were used for estimating α_1 on the height function only using the global parameters in Table II.2. For the situation where only one observation was available, the initial values were arbitrarily set at $H_{100} = 1.3$ m and $G = 2$ m² ha⁻¹ at age 4. Based on these estimates, we predicted subsequent stand values and calculated lack of fit statistics (Table II.3).

As expected, increasing numbers of observations available for predicting α_1 resulted in smaller prediction errors. The errors of the height function converged quickly and no additional gain was achieved when more than

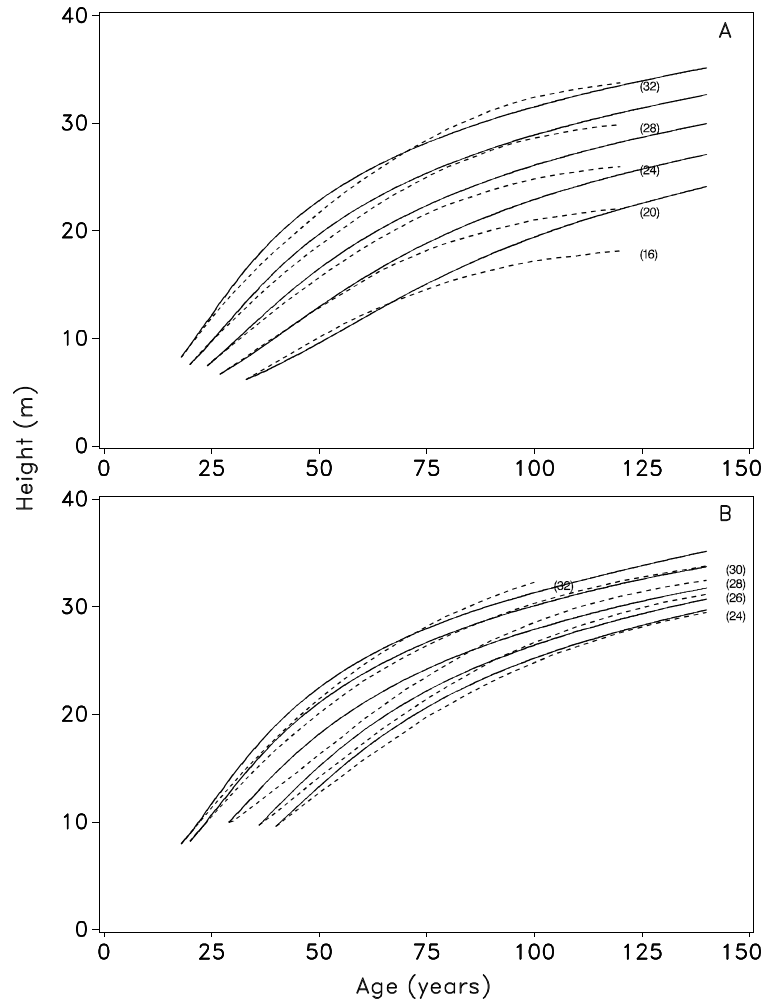


Figure II.4: Plot of H_{100} derived from the yield tables by Møller (1933, A) and Henriksen and Bryndum (1996, B) (dotted lines) and the corresponding values simulated by the dynamic model (full lines). Simulations are started at the first observation of the yield table, using the prescribed reductions in stem numbers and basal area derived from the yield table. Site index (height at age 100) are provided in parenthesis.

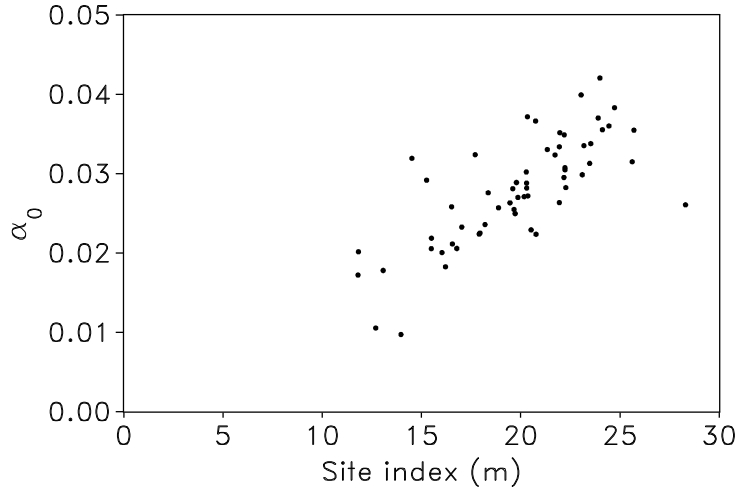


Figure II.5: site-specific parameters (α_0) estimated for each experiment plotted against site index (dominant height at age 50).

Table II.3: Statistics for predicted stand values based on different numbers of available observations (p). Average absolute bias (AAB), average bias (AB), and root mean square error (RMSE) are calculated from the deviations between predicted and observed values at the end of the growth periods. For comparison statistics are calculated for predictions based on site index (dominant height at age 50), using the linear relation between SI and the site-specific parameter.

p	H_{100}			G		
	AB	AAB	RMSE	AB	AAB	RMSE
1	-0.514	0.799	1.054	-1.397	1.740	2.466
2	0.141	0.631	0.850	0.404	1.307	1.805
3	0.091	0.556	0.768	0.267	0.906	1.279
4	0.111	0.568	0.780	0.324	0.812	1.118
5	0.104	0.576	0.781	0.295	0.783	1.050
6	0.075	0.577	0.783	0.190	0.712	0.931
SI	-0.019	0.495	0.692	0.033	0.626	0.864

3 observations were available. The errors of the basal error function converged more slowly and the gain of having 6 observations instead of 5 was 11% improvement in RMSE. When information on basal area was available, additional improvements were observed when α_1 was estimated from the simultaneous height and basal area equations. The superior performance of the model when the site-specific parameter was estimated from site index is probably due to the fact that site index was estimated from all available observations.

Conclusions

The signs of the parameter estimates generally confirmed the anticipated growth paths of dominant height and basal area. Although statistical tests indicated significant systematic deviations between observed and predicted values, the deviations were small and of little practical importance. Cross validation procedures indicated that the model may be applied across a wide range of growth conditions and thinning practises in Denmark without significant loss of precision. In practical application, the site-specific parameter may be estimated locally from site index or from height and basal area observations of that particular site.

The dynamic model provides a flexible tool for predicting stand level growth for a wide range of silvicultural treatments. Hence, stand growth modelling based on the state-space approach represent a significant leap forward from the static yield tables. The model concept further allows for continuous update of the site-specific parameter as more data is obtained for the particular stand and thus allows for changes in growth potential e.g. due to climate change.

References

- Bailey, R. L. and Clutter, J. L. (1974). Base-age invariant polymorphic site curves. *For. Sci.*, 20:155–159.
- Bertalanffy, L. v. (1957). Quantative laws in metabolism and growth. *Quart. Rev. Biol.*, 32:217–231.
- Borders, B. E. and Bailey, R. L. (1986). A compatible system of growth and yield equations for slash pine fitted with restricted three-stage least squares. *For. Sci.*, 32:185–201.
- Cao, Q. V. (2000). Prediction of annual diameter growth and survival for individual trees from periodic measurements. *For. Sci.*, 46:127–131.

- Cao, Q. V. (2004). Annual tree growth predictions from periodic measurements. Gen. Tech. Rep. SRS-71, U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC. 600 p.
- Cieszewski, C. J. and Bailey, R. L. (2000). Generalized algebraic difference approach: theory based derivation of dynamic site equations with polymorphism and variable asymptotes. *For. Sci.*, 46:116–126.
- Clutter, J. L. (1963). Compatible growth and yield models for loblolly pine. *For. Sci.*, 9:354–371.
- Dent, J. B. and Blackie, M. J. (1979). *Systems Simulation in Agriculture*, pages 94–117. Applied Science Publishers ltd., London. 180 p.
- Freese, F. (1960). Testing accuracy. *For. Sci.*, 6:139–145.
- García, O. (1983). A stochastic differential equation model for height growth of forest stands. *Biometrics*, 39:1059–1072.
- García, O. (1994). The state-space approach in growth modelling. *Can. J. For. Res.*, 24:1894–1903.
- Gompertz, B. (1832). On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Phil. Trans. Roy. Soc. London*, 123:513–585.
- Gram, J. P. (1879). Om Konstruktion af Normal-Tilvækstoversigter, med særligt Hensyn til lagttagelserne fra Odsherred. *Tidsskrift for Skovbrug*, 3:207–270. Denmark.
- Hann, D. W. and Hanus, M. L. (2002a). Enhanced diameter-growth-rate equations for undamaged and damaged trees in Southwest Oregon. Research Contribution 39, Forest Research Lab, College of Forestry, Oregon State University. 54 p.
- Hann, D. W. and Hanus, M. L. (2002b). Enhanced height-growth-rate equations for undamaged and damaged trees in Southwest Oregon. Research Contribution 41, Forest Research Lab, College of Forestry, Oregon State University. 38 p.
- Henriksen, H. A. and Bryndum, H. (1996). Bøgeforryngelser i Stagsrode Skov. In Skovsgaard, J. P. and Morsing, M., editors, *Bøgeselvforryngelser i Østjylland*, The Research Series no. 13, pages 5–162. Danish Forest and Landscape Research Institute, Denmark. 215 p.
- Jakobsen, N. K. (1976). Natural-geographical regions of Denmark. *Geografisk Tidsskrift*, 75:1–7.

- Johannsen, V. K. (1999). *A growth model for oak in Denmark*. PhD thesis, Royal Veterinary and Agricultural University. Copenhagen, Denmark. 197 p.
- Johannsen, V. K. (2002). Selection of diameter-height curves for even-aged oak stands in Denmark. Dynamic growth models for Danish forest tree species, Working paper 16, Danish Forest and Landscape Research Institute, Hørsholm, Denmark. 70 p.
- Larsen, P. H. and Johannsen, V. K. (2002). *Skove og Plantager 2000*. Statistics Denmark, Centre for Forest, Landscape and Planning, Danish Forest and Nature Agency, Denmark. 171 p.
- Leary, R., Nimerfro, K., Brand, M. H. G., Burk, T., Kolka, R., and Wolf, A. (1997). Height growth modelling using second order differential equations and the importance of initial height growth. *For. Ecol. Man.*, 97:165–172.
- Lynch, T. B. and Moser Jr., J. W. (1986). A growth model for mixed species stands. *For. Sci.*, 32:697–706.
- MacKinney, A. L. and Chaiken, L. E. (1939). Volume, yield, and growth of loblolly pine in the mid-atlantic coastal region. Tech. Note 33, U.S. Dep. Agric. For. Serv., Appalachian For. Exp. Stn., Asheville, N.C. 30 p.
- McDill, M. E. and Amateis, R. E. (1992). Measuring forest site quality using the parameters of a dimensionally compatible height growth function. *For. Sci.*, 38:409–429.
- McDill, M. E. and Amateis, R. E. (1993). Fitting discrete-time dynamic models having any time interval. *For. Sci.*, 39:499–519.
- Mitscherlich, E. A. (1919). *Landwirtschaftliche Jahrbücher*, 53:167–182.
- Møller, C. M. (1933). Boniteringstabeller og Bonitetsvise Tilvækstoversigter for Bøg, Eg og rødgran i Danmark. *Dansk Skovforenings Tidsskrift*, 18:537–623.
- Møller, C. M. and Nielsen, J. (1953). Afprøvning af de Bonitetsvise Tilvækstoversigter af 1933 for Bøg, Eg og Rødgran i Danmark. *Dansk Skovbrugs Tidsskrift*, 38:1–167.
- Näslund, M. (1936). Skogsforsöksastaltens gallringsforsök i tallskog. *Meddelanden från Statens Skogsforsöksanstalt*, 29:1–169.
- Reynolds, M. R. (1984). Estimating the error in model predictions. *For. Sci.*, 30:454–469.
- Richards, F. J. (1959). A flexible growth equation for empirical use. *Journal of Experimental Botany*, 10:290–300.

- SAS Institute Inc. (1993). *SAS/ETS[®] User's guide, version 6*. Cary, N.C., second edition. 554 p.
- Seber, G. A. F. and Wild, C. J. (1989). *Nonlinear Regression*. Wiley series in probability and mathematical statistics. Wiley, New York. 768 p.
- Skovsgaard, J. P. and Henriksen, H. A. (1996). Increasing site productivity during consecutive generations of naturally regenerated and planted beech (*Fagus sylvatica* L.) in Denmark. In Spiecker, H., Mielikäinen, K., Köhl, M., and Skovsgaard, J. P., editors, *Growth trends of European forests: Studies from 12 countries*, European Forest Institute. Research Report, Vol. 5., pages 89–97. Springer-Verlag, Berlin Heidelberg. 372 p.
- Spiecker, H., Mielikäinen, K., Köhl, M., and Skovsgaard, J. P., editors (1996). *Growth trends of European forests: Studies from 12 countries*. European Forest Institute. Research Report, Vol. 5. Springer-Verlag, Berlin Heidelberg. 372 p.
- Verhulst, P. F. (1845). Recherches mathématiques sur la loi d'accroissement de la population. *Nouv. mém. de l'Académie Royale des Sci. et Belles-Lettres de Bruxelles*, 18:1–41.
- Verhulst, P. F. (1847). Deuxième mémoire sur la loi d'accroissement de la population. *Mém. de l'Académie Royale des Sci., des Lettres et des Beaux-Arts de Belgique*, 20:1–32.
- Wiedemann, E. (1932). *Die Rotbuche 1931*. Mitteilungen der Preußischen Forstlichen Versuchsanstalt. Verlag M.u.H. Schaper, Hannover, Germany. 189 p.
- Zeide, B. (1993). Analysis of growth equations. *For. Sci.*, 39:594–616.

Paper III

A diameter distribution model for even-aged beech

A diameter distribution model for even-aged European beech in Denmark

Thomas Nord-Larsen ^{*1} and Quang V. Cao ^{†2}

^{*}Danish Centre for Forest, Landscape and Planning, Royal Veterinary and Agricultural University, Hørsholm Kongevej 11, DK-2970 Hørsholm, Denmark

[†]School of Renewable Natural Resources, Louisiana State University Agricultural Center, Baton Rouge, LA 70803, USA

Abstract

We developed a diameter distribution model for even-aged stands of European beech in Denmark using the Weibull distribution. The model was estimated using a large dataset from permanent sample plots covering a wide range of different treatments. Parameters of the model were estimated by fitting the cumulative density function using a non-linear least squares procedure. Further, a model constrained to yield estimates consistent with observed basal area was also developed. Predicted distributions confirmed the expected development of diameter distributions in even-aged beech stands. Due to large differences in initial stem-numbers care should be taken when the model is applied to young stands (<40 years).

Keywords: Weibull, CDF regression, *Fagus sylvatica*

Introduction

Forest growth modelling has been an intrinsic part of forest management planning and research for more than two centuries. The majority of models operates at the stand-level and predicts stand-level variables such as basal area or dominant height to provide information needed to estimate harvesting costs, expected yield, financial results etc. Although such models have proved invaluable for forest managers they remain crude simplifications of reality. Recent advances in forest growth modelling have forwarded increasingly complex models operating at the individual-tree level, explicitly modelling complex interactions between trees and their surrounding environment. Although such models represent a significant leap forward in our understanding of the processes of tree growth, they may prove to be of little practical value to forest managers because the detailed measurements required for the implementation of these models are complicated and costly to obtain.

¹Corresponding author. *E-mail address:*tnl@kvl.dk

²*E-mail address:*qciao@lsu.edu

Bridging the gap between crude stand-level simplifications and complex individual tree models, size distribution models are potent tools for providing more detailed knowledge on the forest structure, product mix, product value, and forest operations costs for forest managers and researchers, without additional inventory costs. The size distribution model is often estimated by the parameter recovery approach, in which the parameters of a desired family of distributions are related to stand-level characteristics such as age, site index and stand density (Clutter and Bennett, 1965; Bailey, 1980). In practical application, overall stand attributes may then be disaggregated into more detailed resolutions to provide the forest manager with more detailed information.

From a practical perspective it is desirable that the same family of functions can be used throughout a stand's life and only the parameters need to be changed regardless of initial spacing or differing thinning practices. This necessitates a flexible function but at the same time it is desirable that the function is both parsimonious and easy to estimate. In one of the first studies on size distributions de Liocourt (1898) suggested that the diameter distribution of natural forests may be described by an inverse J-shaped distribution, which was later formulated as a negative exponential function (Meyer, 1933).

In even-aged stands most modellers have recognized that size distributions are non-normal. However, an example of a flexible application of the normal distribution is the Gram-Charlier distribution which consists of an, in principle, infinite series of normal distributions (Prodan, 1953). The simplest, yet more flexible, alternative to the normal distribution is the three-parameter log-normal which is described completely by the mean and variance of the sample, when the origin is known or assumed a priori (Bliss and Reinker, 1964). Adding to the flexibility but also to the complexity of the size distribution model, the Gamma-distribution and the Pearl-Reed growth curve have been fitted to loblolly pine data (Nelson, 1964).

In the first attempt to develop a size distribution model, the beta distribution was fitted to slash pine data by Clutter and Bennett (1965). Keeping the location and range parameters fixed, they estimated the two shape parameters from age, stem number and site index. The beta distribution was later used to characterize observed distributions in beech (Kennel, 1972). The simpler, yet highly flexible two- and three-parameter Weibull distributions are probably the most widely applied functions for modelling tree size distributions and were first used for this purpose by Bailey and Dell (1973). They have been used for predicting the size distribution of Douglas fir (Knowe and Stein, 1995), eastern cottonwood (Knowe et al., 1994), Scots pine (von Gadow, 1984; Sarkkola et al., 2005), black spruce (Newton et al., 2005), slash pine (Schreuder et al., 1979), loblolly pine (Borders and Patterson, 1990; Cao, 2004; Matney and Sullivan, 1982), jack pine (Bailey and Dell, 1973) and different species mixtures (Siipilehto, 1999; Chen, 2004).

Even more flexible, but also more complex, the four-parameter Johnson's S_B distribution has been used to model the distributions of Norway spruce (Tham, 1988), Sitka spruce (Skovsgaard, 1997), Changbai larch (Rennolls and Wang, 2005), and loblolly pine (Hafley and Buford, 1985; Scolforo et al., 2003).

Despite the evident efficacy of size distribution models, no such model is presently available for beech (*Fagus sylvatica* L.) forest management planning or research in Denmark. Hence, the objective of this study was to develop a diameter distribution model for even-aged beech based on a large permanent sample plot data.

Materials

Data was collected from 1872 to 2005 from 69 permanent spacing, species and thinning experiments in European beech, totalling 204 individual plots. Plot sizes varied between 0.07 and 2.65 ha with an average of 0.40 ha. Plots were measured at every thinning, identifying crop trees as well as trees to be thinned. The number of measurement occasions totals 2007. The experiments were located in most parts of Denmark and covered a wide range of site and growth conditions.

All plots were essentially even-aged and mono-specific, covering a wide range of different treatments in terms of initial spacing and thinning regimes. In the thinning experiments, treatments ranged from unthinned controls to heavily thinned shelterwoods. Some plots were managed according to specific thinning strategies, such as group- or selection-thinning, and others were managed according to the thinning strategy typical at the time. Although thinning intervals ranged from 1 to 35 years, the majority of plots were thinned every 4-6 years.

In most of the sample plots, trees were numbered, marked permanently at breast height (1.3 m) and recorded individually. On 451 measurement occasions carried out before 1930 and in some young stands with high stem numbers, trees were recorded in tally lists to 1-cm diameter classes (or 1-inch diameter classes before 1901). In 13 very young stands with high stem numbers, only a subset of stems were measured, e.g. every fifth or tenth row. Breast height diameters were generally obtained by averaging two perpendicular calliper readings. Observations also included records on whether the tree was alive or dead at the time of measurement. Height measurements were typically obtained from about 30 trees per plot.

Based on the paired observations of diameter and height, diameter-height equations were developed for each plot and measurement combination using a modified Näslund-equation (Näslund, 1936; Johannsen, 2002):

$$h = 1.3 + \left(\frac{d}{\alpha + \beta \cdot d} \right)^3 \quad (\text{III.1})$$

where d is diameter at breast height, h is tree height and α and β are parameters to be estimated. The equations were used to estimate the height of trees not measured for height. Dominant height, H_{100} (m), defined as the mean height of the 100 thickest trees per hectare, was calculated for each plot and measurement combination. Where stem numbers were less than 100 per hectare, H_{100} was estimated as the mean height.

Stem numbers, N (ha^{-1}), were calculated as the number of individual trees taller than 1.3 m. When trees forked below 1.3 m, each stem was measured individually, but multiple stems from the same root were counted as one tree. Trees were separated into over- and understorey. Trees were considered understorey when their crowns did not reach into the crown space of the canopy trees. Understorey trees were measured less intensively and were thus not included in this study.

Stand basal area, G ($\text{m}^2 \text{ha}^{-1}$), of each plot was estimated by summation of individual tree basal areas calculated from the diameter measurements. When trees were recorded in tally lists, mean class values were used as an estimate of the diameter of all trees in that class. Diameter corresponding to mean basal area, D_g (cm), was derived from the estimates of N and G . The data represent a wide range of stand ages and stand values in terms of H_{100} , G , D_g and N (Figure III.1).

Methods

The Weibull distribution (Weibull, 1951):

$$f(x) = (c/b) \left((x-a)/b \right)^{c-1} e^{-((x-a)/b)^c}; x \geq a, b > 0, c > 0. \quad (\text{III.2})$$

covers most of the desired shapes for a diameter distribution model. It describes the inverse J-shape for $c < 1$ and the exponential distribution for $c = 1$. For $1 < c < 3.6$ the density function is mound shaped and positively skewed and for $c = 3.6$ the density function becomes approximately normal. If $c > 3.6$ the density function becomes increasingly negatively skewed. Contrasting the flexibility of the Weibull distribution, mathematical derivations are simple and allow for simple solutions in simulation studies (Weibull, 1951). Motivated by a comparison of skewness and kurtosis observed on the individual measurement occasions and the possible combinations of the Weibull distribution (Figure III.2) as well as the simplicity of the Weibull distribution and its well-described properties, this function was used for modelling the diameter distribution of European beech in Denmark.

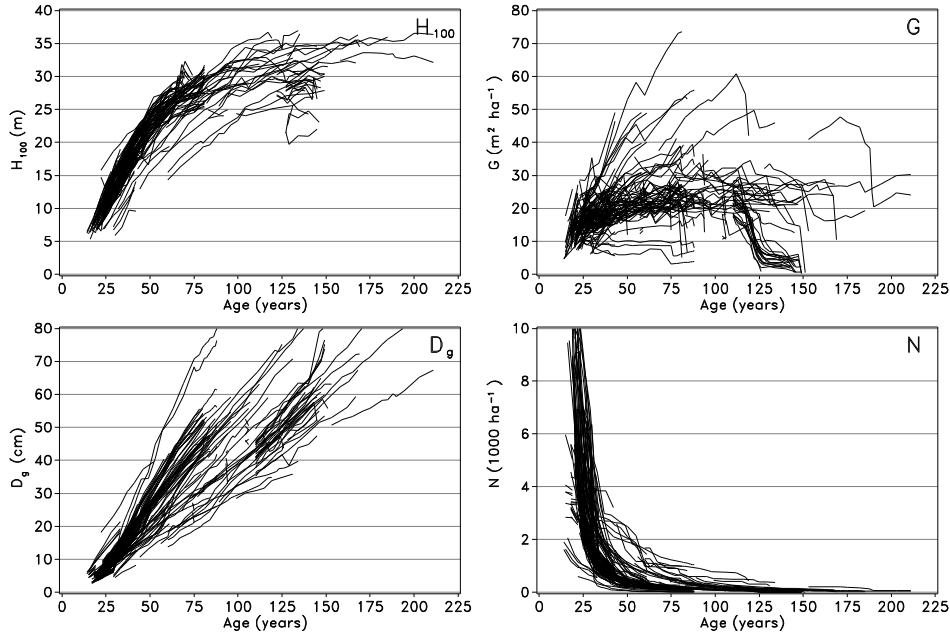


Figure III.1: Stand-level values of H_{100} (A), G (B), D_g (C) and N (D). The lines represent repeated measurements on each individual plot.

Model estimation

Parameters of the Weibull distribution may be estimated using various kinds of transformations to linearize the function and subsequent estimation by (weighted) linear regression, or by moment (Burk and Newberry, 1984) or percentile estimation (Bailey and Burgan, 1989; Borders and Patterson, 1990). Estimation of the parameters by maximum likelihood has been found to produce consistently better goodness-of-fit statistics compared to the previous methods, but also put the largest demands on the computational resources (Cao, 2004). Recently, parameters of the Weibull distribution were iteratively searched to minimize the squared deviations between the observed and predicted cumulative distribution function (cdf) (CDF-regression; Cao, 2004). CDF-regression was found to yield the best goodness-of-fit statistics among the methods tested in this study.

The cumulative distribution function of the Weibull distribution is:

$$F(x_{ij}) = 1 - \exp\left(-\left(\frac{x_{ij} - a}{b}\right)^c\right) \quad (\text{III.3})$$

where F_{ij} is the cumulative probability for diameter at breast height (x_{ij}) of the i th tree in the j th plot and age combination. In this study, the parameters of the Weibull distribution were initially estimated for each

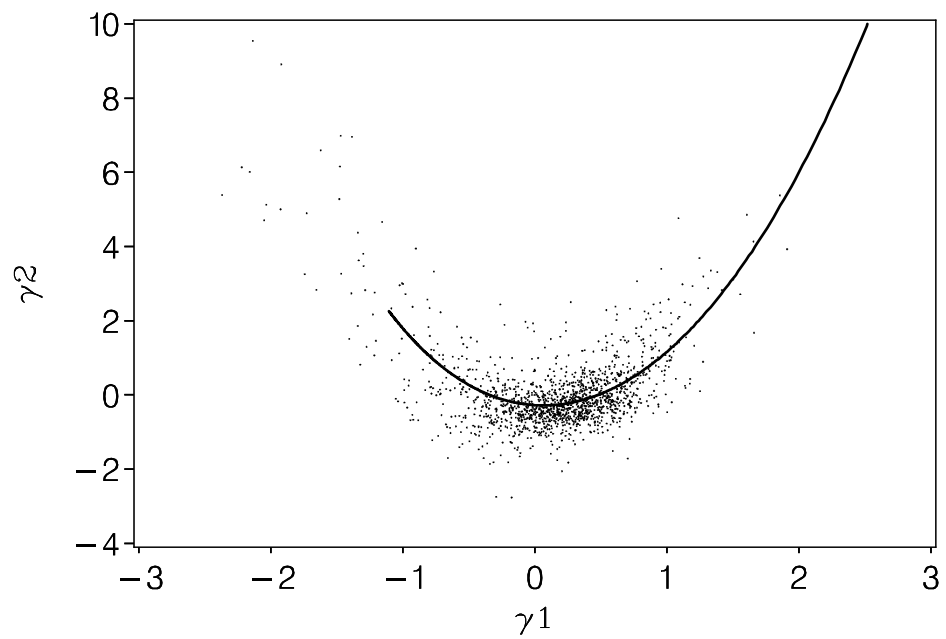


Figure III.2: Skewness (γ_1) and kurtosis (γ_2) of observed diameter distributions compared with the possible solutions of the Weibull distribution (full line).

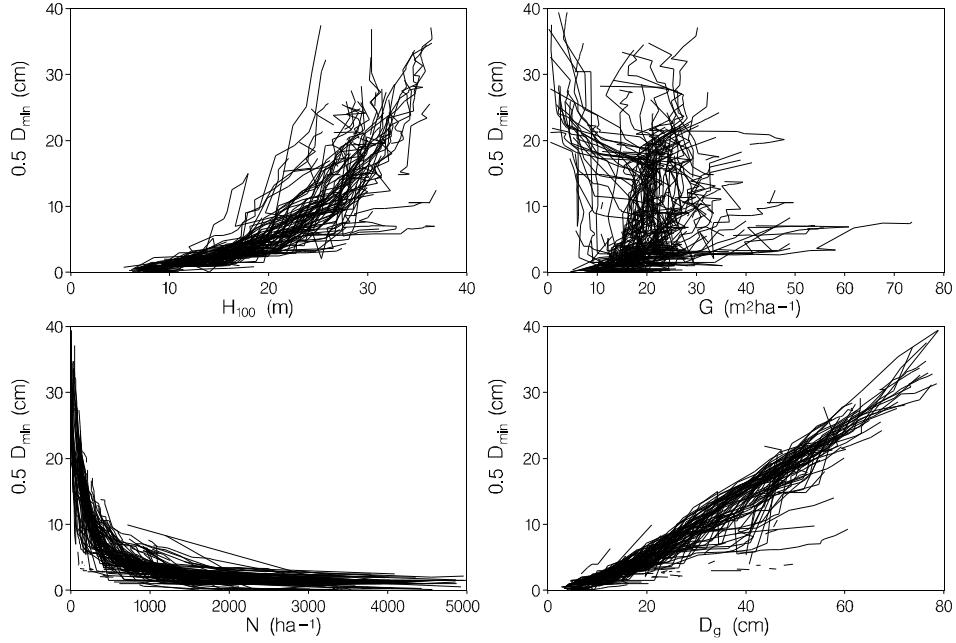


Figure III.3: *A priori* estimates of the location parameter ($0.5D_{min}$) for the individual plots and measurement occasion plotted against dominant height (H_{100}), basal area (G), stem number (N) and quadratic mean diameter (D_g).

age and plot combination using CDF-regression. The parameters were iteratively searched to minimize:

$$\sum_{j=1}^p \sum_{i=1}^{n_j} \frac{(F_{ij} - \widehat{F}_{ij})^2}{n_i} \quad (\text{III.4})$$

Due to high levels of correlations between parameters, estimation of the individual cdf's in this preliminary analysis frequently failed to converge. We therefore used 0.5 times the observed minimum diameters (D_{min}) of the different measurement occasions as an *a priori* estimate of the location parameter a (Figure III.3).

Based on a graphical analysis of $0.5D_{min}$ plotted against various stand-level variables as well as statistical analysis of those relations, a was estimated from a Chapman-Richards function of D_g , where the asymptote is D_g and the other parameters were estimated from D_g , H_{100} , and N :

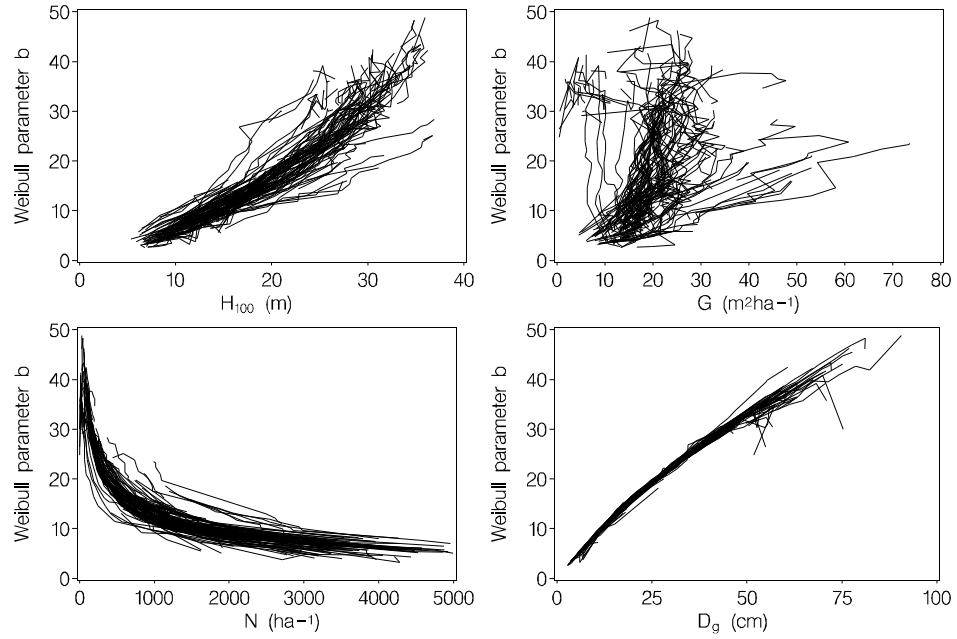


Figure III.4: Estimated b parameter of the Weibull-equation plotted against dominant height (H_{100}), basal area (G), stem number (N) and quadratic mean diameter (D_g).

$$a_j = D_{g,j} \left(1 - \exp(-a_1 D_{g,j}) \right)^{a_2} + \varepsilon_{a,j}, \quad (\text{III.5})$$

$$\begin{aligned} a_1 &= a_{01} D_{g,j} H_{100,j} \\ a_2 &= a_{02} + a_{03} \ln(N_j) \end{aligned}$$

where $a_{01} - a_{03}$ are parameters to be estimated, and $\varepsilon_{a,j} \sim N(0, \sigma_{a,j}^2)$ is the error term. Subscript denotes the j th plot-age combination.

Using the *a priori* estimates of a , the scale (b) and shape (c) parameters were subsequently estimated for each age and plot combination and related to various stand variables (Figure III.4 and III.5).

Based on a graphical analysis of estimates of b and c plotted against observed stand-level variables as well as statistical analyses of those relations, the scale parameter was estimated from a saturation growth model of D_g :

$$b_j = \frac{b_{01} D_{g,j}}{b_{02} + D_{g,j}} + \varepsilon_{b,j} \quad (\text{III.6})$$

where b_{01} and b_{02} are parameters to be estimated and $\varepsilon_{b,j} \sim N(0, \sigma_{b,j}^2)$ is

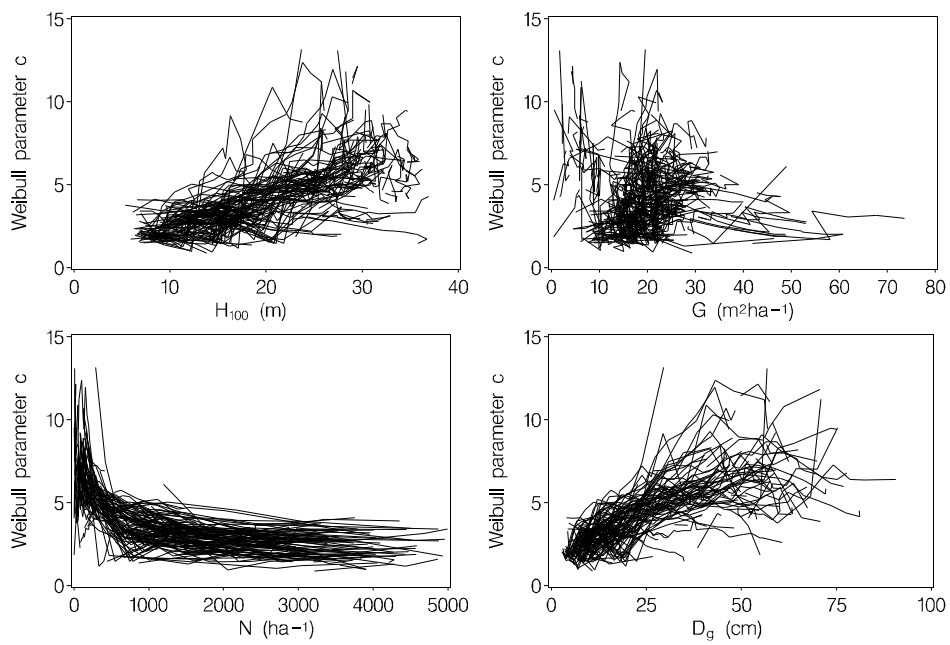


Figure III.5: Estimated c parameter of the Weibull-equation plotted against dominant height (H_{100}), basal area (G), stem number (N) and quadratic mean diameter (D_g).

the error term. The shape parameter was estimated from a logistic function of D_g where the parameters were estimated from H_{100} , and N :

$$c_j = \frac{c_1}{1 + c_2 \exp(-c_3 D_{g,j})} + \varepsilon_{c,j}, \quad (\text{III.7})$$

$$c_1 = c_{01} + c_{02} N_j D_{g,j}^2$$

$$c_2 = c_{03}$$

$$c_3 = c_{04} \frac{D_{g,j}}{H_{100,j}}$$

where $c_{01} - c_{04}$ are parameters to be estimated and $\varepsilon_{c,j} \sim N(0, \sigma_{c,j}^2)$ is the error term.

Based on the initial analyses, the parameters in equations (III.5), (III.6), and (III.7) were estimated simultaneously using CDF-regression as described by Cao (2004). The diameter observations were assumed to be independent, random observations.

Constrained estimation

When the distribution parameters of the Weibull distribution are known for a stand with N trees per hectare, the basal area may be calculated as:

$$\begin{aligned} G_j &= \frac{\pi}{4} N_j c_j b_j^{-1} \int_a^\infty x_{ij}^2 \left(\frac{x_{ij} - a_j}{b_j} \right)^{c_j-1} e^{-\left(\frac{x_{ij} - a_j}{b_j} \right)^{c_j}} dx \\ &= \frac{\pi}{40,000} N_j (a_j^2 + 2a_j b_j \Gamma_1 + b_j^2 \Gamma_2) \end{aligned} \quad (\text{III.8})$$

where $\Gamma_1 = \Gamma(1 + 1/c_j)$, $\Gamma_2 = \Gamma(1 + 2/c_j)$, and $\Gamma(\cdot)$ is the complete Gamma-function. Solving equation (III.8) and substituting for either of the parameters constrain the Weibull distribution to yield estimates consistent with the observed or predicted basal area of a particular stand. In addition to the un-constrained model, we estimated the parameters of equation (III.5) and (III.7), where b_j was constrained to yield estimates of the diameter distribution function, consistent with observed or predicted basal area as:

$$b_j = \frac{-a_j \Gamma_1 + \sqrt{a_j^2 (\Gamma_1^2 - \Gamma_2) + \Gamma_2 D_{g,j}^2}}{\Gamma_2} \quad (\text{III.9})$$

Model evaluation

Estimated diameter distributions were evaluated by statistical tests that included t-tests of predicted mean and χ^2 , Kolmogorov-Smirnoff (KS), and Anderson-Darling (AD) goodness-of-fit tests. Although the KS and AD goodness-of-fit tests may be useful when comparing different families of distributions in the early stages of model building, one important caveat apply to the use of these formal tests when evaluating diameter distribution models (Reynolds et al., 1988). Theoretically, the tests only apply to the case where the distribution function is completely specified. This is seldom the case and critical values have been provided for various cases where the parameters must be estimated (Stephens, 1977). However, no critical values have been calculated for the case where parameters are estimated by CDF-regression. We therefore conducted the tests, ignoring the fact that the distribution was not completely specified.

In addition to the goodness-of-fit statistics, the unconstrained diameter distribution model was evaluated by comparing observed basal area to basal area predicted by the diameter distribution model. This comparison was motivated by the importance of basal area in forest applications, and the fact that errors among the large and thereby more valuable trees have more weight.

Finally, we conducted a leave-one-out cross-validation for both the constrained and un-constrained model, where entire experiments were left out one at a time during the estimation procedure. Estimated models were subsequently applied to the left-out experiment and goodness-of-fit statistics were calculated. The stability of estimates was evaluated by comparing the number of rejected distributions to the numbers obtained in the original estimation.

Results

Fitting of the cumulative distribution function accounted for 94.1% of the variation (R^2) and resulted in significant estimates for all parameters (Table III.1). When the model was constrained to yield estimates consistent with the observed basal area, the model accounted for 93.3% of the observed variation.

The basal area predicted by the unrestricted model deviated less than 10% from the observed (Figure III.6), but the model seemed to underestimate basal area systematically.

The null hypothesis, that the estimated mean diameter is similar to the observed mean diameter was rejected for 1.6–2.7% of the 1539 distributions for the un-constrained model (Table III.2). Also for the un-constrained model, 34.8–47.3% of predicted distributions differed significantly from the observed, depending on the applied goodness-of-fit statistic. The number

Table III.1: Parameter estimates and their approximate standard errors of the model fitted by the CDF-method. Estimates are provided for both the un-constrained model and for the model constrained to yield estimates consistent with observed basal area. All parameter estimates were highly significant ($P<0.0001$).

Parameter	Not constrained			Constrained		
	Estimate	Std. err.	t value	Estimate	Std. err.	t value
a_{01}	3.00095E-8	1.25 E-9	23.94	4.38261E-7	2.17 E-8	20.22
a_{02}	0.33278	3.82 E-3	87.09	0.18282	4.84 E-3	37.76
a_{03}	-0.00165	1.74 E-4	-9.49	0.00321	4.81 E-4	6.68
b_{01}	283.13622	5.56	50.93	.	.	.
b_{02}	268.60650	5.18	51.85	.	.	.
c_{01}	9.30607	3.51 E-2	267.81	5.10905	2.12 E-2	240.47
c_{02}	-5.36769E-6	4.26 E-8	-125.88	-3.28411E-6	3.11 E-8	-105.74
c_{03}	3.27888	1.46 E-2	224.92	1.71800	1.12 E-2	152.83
c_{04}	0.07880	2.86 E-4	275.24	0.10277	6.84 E-4	150.32

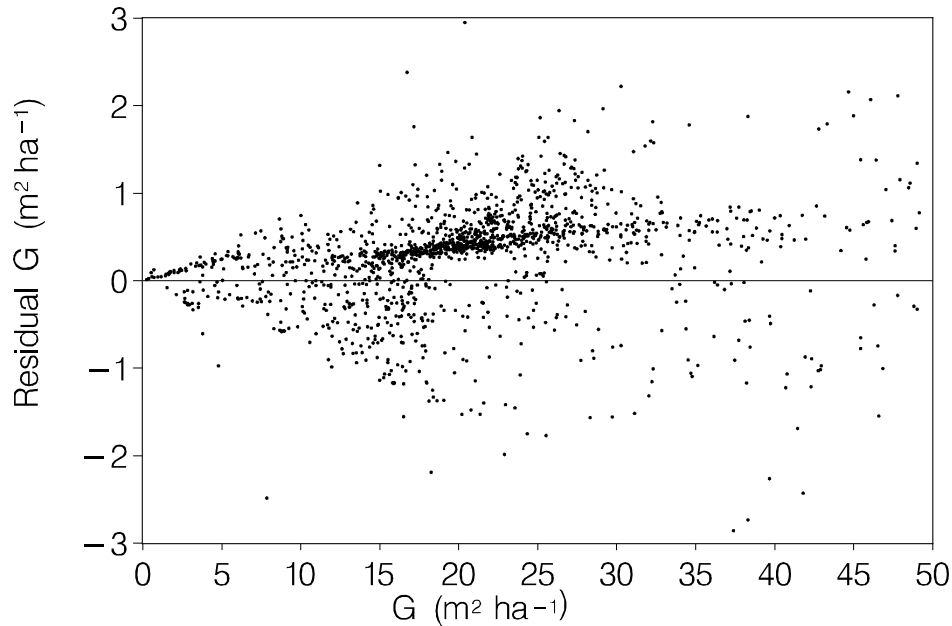


Figure III.6: Residual basal area of the unrestricted diameter distribution model.

of rejected distributions was similar for the constrained model, although this model consistently rejected fewer of the predicted distributions. The leave-one-out cross-validation showed only a small increase in the number of rejected distributions for both the constrained and un-constrained models, which indicated a large stability of the model.

Discussion

Judging from the model predictions, the diameter distribution is typically right skewed in young, even-aged beech stands, probably as a result of self thinning among the smallest trees (Figure III.7). As the stand matures, the peakedness of the distribution is reduced and it becomes less skewed, but the variation increases. Classical thinning from below causes a relative reduction in variation, peakedness and skewness of the distribution. In old beech stands (>100 years) skewness and kurtosis of the diameter distribution begins to increase again. The observed pattern of the diameter distribution is concordant with the findings of a study on even-aged beech stands in Germany (Kennel, 1972) and with findings from southern Sweden (Carbonnier, 1971).

Despite the apparent agreement between expected development of the

Table III.2: Test statistics and the number of predicted distributions significantly different from the observed ($P \leq 0.05$). Test statistics are provided for both the un-constrained and the constrained model as well as for the cross-validation procedure.

Statistic	Not constrained			Constrained			cross-validation		
	Mean	Rejected	%	Mean	Rejected	%	Mean	Rejected	%
Mean	0.242	42	2.7	0.021	25	1.6	0.242	27	2.7
χ^2	56.480	701	47.3	59.035	674	45.5	57.851	708	47.8
K-S.	0.138	536	34.8	0.135	511	33.2	0.139	546	35.5
A.-D.	8.186	609	39.6	8.338	566	36.8	8.446	615	40.0

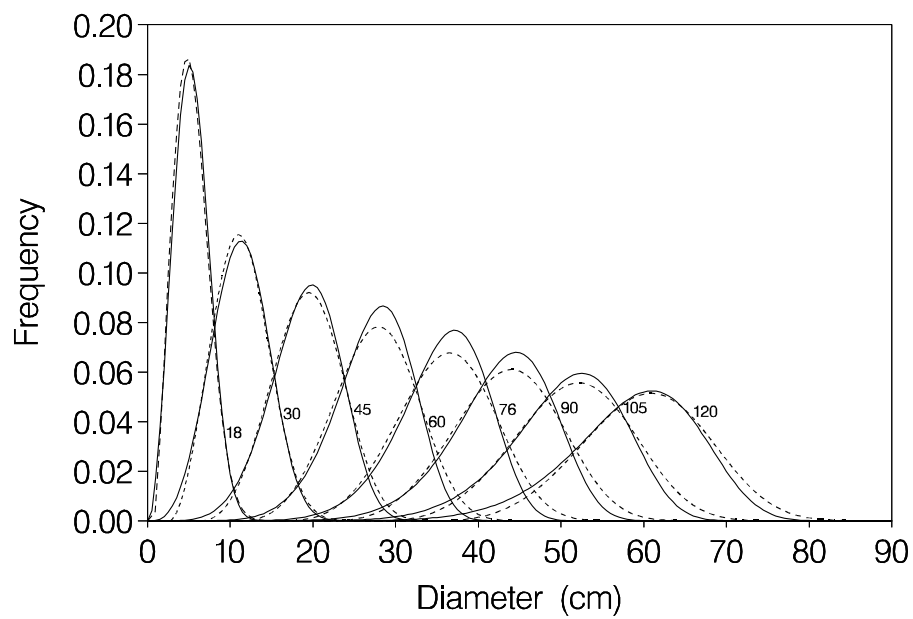


Figure III.7: Simulated development of the diameter distribution for the un-constrained (full line) and constrained model (dashed line). Simulations are based on the most commonly used yield table for beech in Denmark (Møller, 1933). Numbers indicate stand ages.

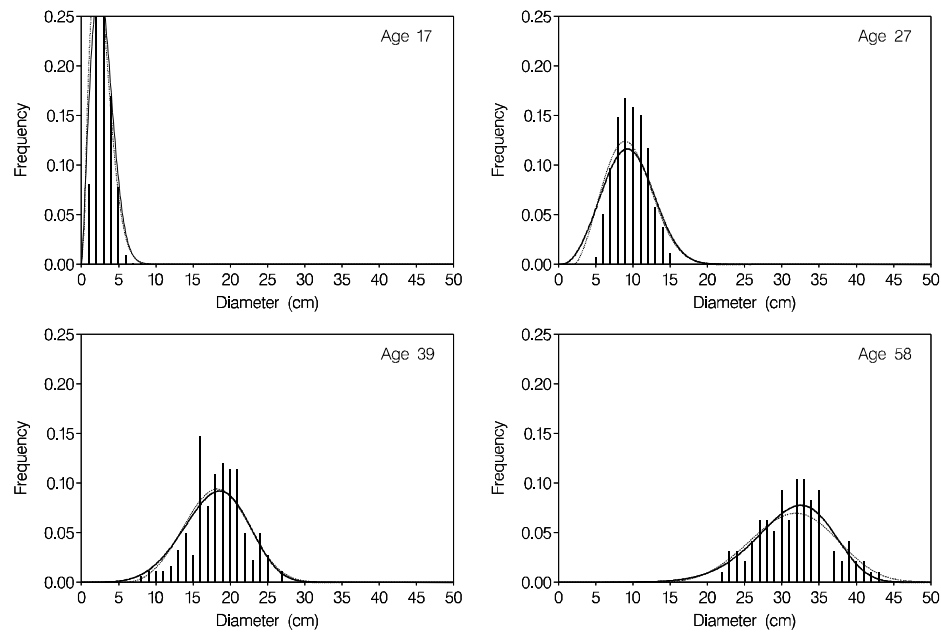


Figure III.8: Simulated diameter distributions of experiment EC (plot 01, C-grade thinning) for the un-constrained (full line) and constrained model (dashed line) compared with the observed diameter distribution.

diameter distribution over time and the model predictions, 30-45% of the predicted distributions differed from the observed distribution according to our criteria at the 5% significance level (for χ^2 , KS and AD-statistics). The seeming weakness of the model is to be expected when fitting a smooth curve to diameter distributions from managed stands. In this case, diameter distributions result from a process that is not random. Thinnings are often targeted at specific social classes of trees, or at obtaining specific assortments or a specific stand structure. Hence, certain types of trees are thinned, causing the size distribution to be irregular (Figure III.8). Such diameter distributions would not be successfully fitted by any smooth statistical distribution. This probably explains why stand table projection methods are considered superior to distribution prediction methods when predicting future diameter distributions (Pienaar and Harrison, 1988; Borders and Patterson, 1990; Nepal and Somers, 1992; Cao and Baldwin, 1999).

In a number of plots where observed distributions differed from the predicted, visual inspection showed that observed distributions tended to be bi-modal, possibly because the separation of over- and understorey trees was not always successful. The Weibull distribution is uni-modal and is thus unsuited to model such distributions. Bi-modal diameter distributions have been modelled by finite mixtures of various distributions (for a forestry

related application, see Skovsgaard, 1997; Liu et al., 2002). However, in this study we decided not to model the distribution of understorey trees for two reasons. Firstly, the understorey trees were measured less intensively and it was uncertain if all understorey trees were in fact measured in the historical data. Secondly, understorey trees have been treated very differently across the individual plots, but their treatment has little effect on stand-level variables such as basal area or dominant height. Hence, the diameter distribution model cannot be expected to adequately model the distribution of understorey trees based on stand-level variables.

Further analyses showed that the frequency of predicted distributions that differed significantly from the observed was highest among young age classes (Figure III.9). This reflects a general problem of all diameter distribution models: that prior treatment influences the diameter distribution, but is not entailed in the model since such information is generally not available for its application. In other words, we model the diameter distribution based on the assumption that all information needed is expressed by the stand variables, although these may reflect many different thinning strategies that result in different diameter distributions. This becomes especially evident for young stands since initial conditions (i.e. stem numbers) differ considerably between, for example a naturally regenerated stand with several hundred thousand plants per hectare and a planted stand with less than 5,000 plants per hectare. Such stands are not likely to have similar diameter distributions, even if they are thinned to approximately the same stem number or basal area. Later, the frequency of failed estimates is reduced because multiple thinnings according to a similar strategy even out initial differences but probably also because stem numbers are reduced and the estimated distribution therefore becomes harder to reject.

Conclusion

The diameter distribution model was successfully estimated using CDF-estimation and predicted distributions confirmed the expected development of diameter distributions in even-aged beech stands. However, predicted distributions deviated significantly from the observed in 60-80% of stands younger than 40 years, probably due to large differences in initial stem-numbers. Hence, the diameter distribution model may be used for predicting distributions from observed or predicted stand-level values of stem numbers and basal area, but care should be taken when the model is applied to young stands (<40 years).

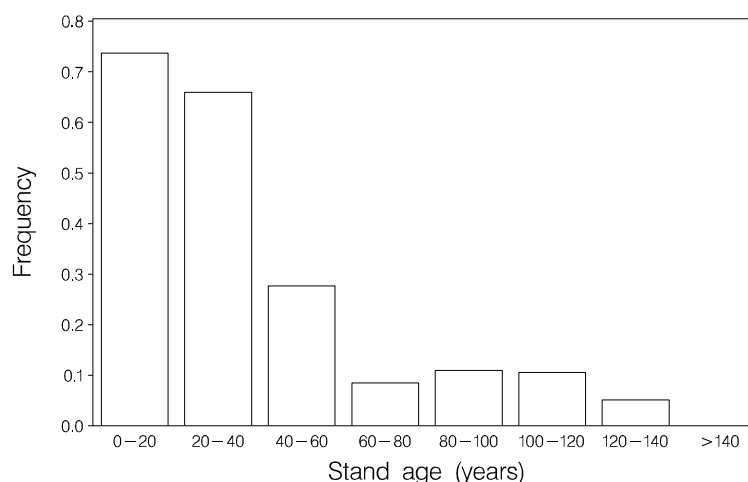


Figure III.9: Frequency of failed experiments according to the Kolmogorov-Smirnoff-test in different age-groups.

References

- Bailey, R. L., 1980. Individual tree growth derived from diameter distribution models. *For. Sci.* 26, 626–632.
- Bailey, R. L., Burgan, T. M., 1989. Fertilized midrotation-aged slash pine plantations - stand structure and yield prediction models. *South. J. Appl. For.* 13, 13–17.
- Bailey, R. L., Dell, T. R., 1973. Quantifying diameter distributions with the Weibull function. *For. Sci.* 19, 97–104.
- Bliss, C. I., Reinker, K. A., 1964. A lognormal approach to diameter distributions in even-aged stands. *For. Sci.* 10, 350–360.
- Borders, B. E., Patterson, W. D., 1990. Projecting stand tables: A comparison of the Weibull diameter distribution method, a percentile-based projection method, and a basal area growth projection method. *For. Sci.* 36, 413–424.
- Burk, T. E., Newberry, J. D., 1984. A simple algorithm for moment-based recovery of Weibull distribution parameters. *For. Sci.* 30, 329–332.
- Cao, Q. V., 2004. Predicting parameters of a Weibull function for modelling diameter distribution. *For. Sci.* 50, 682–685.
- Cao, Q. V., Baldwin, V. C., 1999. A new algorithm for stand table projection models. *For. Sci.* 45, 506–511.

-
- Carbonnier, C., 1971. Bokens produktion i Södra Sverige. *Studia Forestalia Suecica* 91, 1–89.
- Chen, W. J., 2004. Tree size distribution functions of four boreal forest types for biomass mapping. *For. Sci.* 50, 436–449.
- Clutter, J. L., Bennett, F. A., 1965. Diameter distribution in old-field slash pine plantations. Report 13, Ga. For. Res. Counc., 9 p.
- de Liocourt, F., 1898. De l'aménagement des sapinières. *Bulletin trimestriel* 4, Société Forestière de Franche-Comté et Belfort, 645 p.
- Hafley, W. L., Buford, M. A., 1985. A bivariate model for growth and yield prediction. *For. Sci.* 31, 237–247.
- Johannsen, V. K., 2002. Selection of diameter-height curves for even-aged oak stands in Denmark. Dynamic growth models for Danish forest tree species, Working paper 16, Danish Forest and Landscape Research Institute, Hørsholm, Denmark, 70 p.
- Kennel, R., 1972. Die Buchendurchforstungsversuche in Bayern von 1870 bis 1970. *Forschungsberichte* 7, Forstliche Forschungsanstalt München, München, Germany, 264 p.
- Knowe, S. A., Foster, G. S., Roussau, R. J., Nance, W. L., 1994. Eastern cottonwood clonal mixing study: predicted diameter distributions. *Can. J. For. Res.* 24, 405–414.
- Knowe, S. A., Stein, W. I., 1995. Predicting the effects of site preparation and protection on development of young Douglas-fir plantations. *Can. J. For. Res.* 25, 1538–1547.
- Liu, C., Zhang, L., Davis, C. J., Solomon, D. S., Gove, J., 2002. A finite mixture model for characterizing the diameter distribution of mixed-species forest stands. *For. Sci.* 48, 653–661.
- Matney, T. G., Sullivan, A. D., 1982. Compatible stand and stock tables for thinned and unthinned loblolly pine stands. *For. Sci.* 28, 161–171.
- Meyer, H., 1933. Eine mathematisch-statistische Untersuchung über den Aufbau des Plenterwaldes. *Schweizerische Zeitschrift für Forstwesen* 84, 33–46, 88–103, 124–133.
- Møller, C. M., 1933. Boniteringstabeller og Bonitetsvise Tilvækstoversigter for Bøg, Eg og rødgran i Danmark. *Dansk Skovforenings Tidsskrift* 18, 537–623.
- Näslund, M., 1936. Skogsforsöksanstaltens gallringsforsök i tallskog. *Meddelanden från Statens Skogsforsöksanstalt* 29, 1–169.

- Nelson, T. C., 1964. Diameter distribution and growth of loblolly pine. *For. Sci.* 10, 105–114.
- Nepal, S. K., Somers, G. L., 1992. A generalized approach to stand table projection. *For. Sci.* 38, 120–133.
- Newton, P. F., Lei, Y., Zhang, S. Y., 2005. Stand-level diameter distribution yield model for black spruce plantations. *For. Ecol. Man.* 209, 181–192.
- Pienaar, L. V., Harrison, W. M., 1988. A stand table projection approach to yield prediction in unthinned even-aged stands. *For. Sci.* 34, 804–808.
- Prodan, M., 1953. Die Verteilung des Vorrates gleichaltriger Hochwaldbestände auf Durchmesserstufen. *Allgemeine Forst- und Jagdzeitung* 124, 93–106.
- Rennolls, K., Wang, M., 2005. A new parameterization of Johnson's S_B distribution with application to fitting forest tree diameter data. *Can. J. For. Res.* 35, 575–579.
- Reynolds, M. R., Burk, T. E., Huang, W.-C., 1988. Goodness-of-fit tests and model selection procedures for diameter distribution models. *For. Sci.* 34, 373–399.
- Sarkkola, S., Hökkä, H., Laiho, R., Päivänen, J., Penttilä, T., 2005. Stand structural dynamics on drained peatlands dominated by Scots pine. *For. Ecol. Man.* 206, 135–152.
- Schreuder, H. T., Hafley, W. L., Bennet, F. A., 1979. Yield prediction for unthinned natural slash pine stands. *For. Sci.* 25, 25–30.
- Scolforo, J. R. S., César, F., Tabai, V., de Macedo, R. L. G., Jr., F. W. A., de Assis, A. L., 2003. S_B distributions's accuracy to represent the diameter distribution of *Pinus taeda*, through five different fitting methods. *For. Ecol. Man.* 175, 489–496.
- Siipilehto, J., 1999. Improving the accuracy of predicted basal-area diameter distribution in advanced stands by determining stem number. *Silva Fennica* 33, 281–301.
- Skovsgaard, J. P., 1997. Tyndingsfri drift af sitkagran. Forskningsserien no. 19. Forskningscentret for Skov & Landskab, Hørsholm, Denmark, 525 p.
- Stephens, M. A., 1977. Goodness-of-fit for the extreme value distribution. *Biometrika* 64, 583–588.
- Tham, Å., 1988. Structure of mixed *Picea abies* (L.) Karst. and *Betula pendula* Roth. and *Betula pubescens* Ehrh. stands in south and middle Sweden. *Scandinavian Journal of Forest Research* 3, 355–370.

von Gadow, K., 1984. Die Erfassung von Durchmesserverteilungen in gleichaltrigen Kiefernbeständen. Forstwissenschaftliches Centralblatt 103, 360–374.

Weibull, W., 1951. A statistical distribution function of wide applicability. Journal of Applied Mechanics 18, 293–297.

Paper IV

Modelling individual-tree
growth

Modelling individual-tree growth from data with highly irregular measurement intervals

Thomas Nord-Larsen ^{*1}

^{*}Royal Veterinary and Agricultural University
Forest & Landscape
Hørsholm Kongevej 11, DK-2970 Hørsholm, Denmark

Abstract

Fitting annual tree growth and survival models to data with irregular measurement intervals requires special consideration to the interpolation of the independent variables. This study presents an iterative method for continuously updating individual-tree and stand attributes, using the hypothesised functional form of a system of forward difference equations. Based on data from permanent sample plots, parameter estimates were obtained for three first-order difference equations of diameter and height growth and mortality for European beech in Denmark.

One parameter of the individual-tree diameter and height growth models was estimated locally and expresses apparent site quality. The plot-specific parameters of the individual-tree growth models were highly correlated with site index and plot-specific estimates of rate constants from a dominant height growth model. Parameter estimates of individual-tree models based on either of those indicators of site quality allow for a flexible use of the models. The study failed to establish any relation between plot-specific rate constants and soil texture variables. The resulting system of individual-tree models is consistent with tree growth and mortality expected for beech in Denmark.

Keywords: *Fagus sylvatica*, difference equation, diameter, height, mortality

Introduction

Difference equations are suitable for describing processes that involve discrete periods of change, such as growth periods, and have been widely used in forest growth modelling. The difference form of the growth equation is generally simpler than its closed form and may describe complex responses using relatively simple functional forms. In addition, the dynamic nature of such equations allows for user-specific silvicultural treatment regimes, because initial values are allowed to change at the beginning of each new prediction cycle. Further, when growth conditions are changing through

¹Corresponding author. E-mail: tnl@kvl.dk, Phone: (+45) 35281758, Fax: (+45) 35271517

the life of the forest stand, or when new information is obtained for the modelling subject, the model allows for continuous updating of site-specific variables.

When fitting difference equations, modellers of forest growth are often faced with the problem that the time interval between measurements does not match the desired interval for the growth model. This is always the case when the measurement intervals differ between observations and then interpolation or even extrapolation is necessary to provide a consistent growth interval throughout the data. The simplest way to deal with discrepancies between actual and desired measurement intervals is to assume that the periodic increment is constant between measurements and equals the average growth rate. Then periodic growth rates may be estimated by linear interpolation between measurements and fitted to the state variables at the beginning of the measurement interval. However, in case of a concave increment trajectory, the assumption of constant growth rates leads to underestimation of annual growth, whereas the opposite is true when the increment trajectory is convex (McDill and Amateis, 1993). In an often used form of the interpolation method described above, periodic growth rates are fitted to the state variables projected to the midpoint of the measurement interval by linear interpolation (Clutter, 1963). The rationale underlying this approach is that the average growth rate is closest to the actual growth rate at the midpoint of the measurement interval. This methodology was discussed by Clutter (1963), who noted that the assumption that average periodic growth may be used as instantaneous growth will introduce errors because growth processes are almost certainly nonlinear rather than linear.

To improve the methods for obtaining parameter estimates of growth models, McDill and Amateis (1993) suggested that correction for the difference between observed and desired time interval in the difference equation should be made in concordance with the specified growth function. This approach was adopted by Cao (2000), who estimated annual individual diameter increment and survival by incrementing annual growth and probabilities of survival to the state at the end of the measurement interval. Hereby, the growth from each observed starting value was iterated to the corresponding value of the following observation, using the years between individual measurements as the number of iterations. Johannsen (1999) used a similar approach estimating simultaneous systems of equations for diameter and height increment of Norway spruce (*Picea abies* (L.) H. Karst) and oak (*Quercus robur* L. and *Quercus petraea* L.), respectively.

In Denmark, increasing focus on silvicultural regimes that meet the demands for ecological, social, as well as economic goods has led to the ongoing conversion towards near-natural or uneven-aged forestry. This paradigm shift in management of natural resources has created a demand for individual-tree growth models that are able to model the conversion and the much more diverse forest structures expected in the future. European beech (*Fagus syl-*

vatica L.) is one of the most important deciduous forest tree species in Denmark, both in economic terms and when considering the ongoing conversion toward near-natural forestry. Data for developing individual-tree growth models for beech come from permanent sample plots measured at highly irregular intervals. Hence, the objective of this study is to develop non-spatial models of individual diameter and height growth and annual mortality of beech in Denmark, with special consideration to the interpolation of the independent variables, owing to the irregular measurement intervals.

Data

The gross data for developing individual-tree growth models for beech are from 69 permanent spacing, species and thinning experiments in beech and a total of 201 individual plots. Plot sizes vary between 0.07 and 2.65 ha with an average of 0.36 ha. The experiments are located in most parts of Denmark and cover a wide range of different site types and growth conditions. However, the majority of the experiments are situated in the eastern parts of the country where the growth conditions are more suitable for growing beech than the sandy soils in western Denmark.

The data were collected during the years from 1887 to 2005 and the stands were observed for 10 to 103 years. The number of measurement occasions totalled 1580. All the plots were even-aged and mono-specific. The data include a wide range of different treatments in terms of initial spacing and thinning intensities from unthinned controls to heavily thinned stands. Some plots were managed according to other thinning strategies, such as group- or selection-thinning, and others were managed according to the thinning strategy typical at the time.

The permanent sample plots were generally subjected to the frequent thinning regime predominantly used in Denmark, although the intervals between thinnings varied considerably depending on stand age and thinning intensity. As the experiments were generally measured at every thinning occasion, measurement intervals varied from 1 to 35 years, with an average of 3.8 years.

In the sample plots, all trees were numbered, marked permanently at breast height (1.3 m) and recorded individually. Breast height diameters were obtained by averaging two perpendicular calliper readings. Observations also included records on whether the tree was alive or dead at the time of measurement. Diameter measurements were obtained from 89,937 individual trees, covering 197,399 measurement intervals (Table IV.1). Heights of live trees were obtained by means of a hypsometer, and felled trees were measured on the ground using a tape measure. Height measurements were obtained from 6,485 individual trees, covering 19,965 measurement intervals. Finally, soil texture analyses were carried out in 48 experiments, providing

Table IV.1: Summary statistics of individual-tree diameter (d) and height (h) measurements and stand level estimates of dominant height (H_{100}), basal area (G), stem number (N), diameter corresponding to the mean basal area tree (D_g) and age (T).

Variable	Unit	N	Mean	Minimum	Maximum	Std. Dev.
Individual trees						
d	cm	275785	16.65	0.1	108.5	13.81
h	m	34379	20.37	1.3	40.0	7.76
Stand level						
H_{100}	m	1286	22.81	5.08	36.95	7.14
G	m ² ha ⁻¹	1580	20.18	0	73.58	9.69
N	ha ⁻¹	1580	708.61	0	9629.63	1121.54
D_g	cm	1580	33.60	3.28	90.57	18.15
T	years	1580	74.23	14	211	39.23

information on soil texture variables (fractions of clay, silt, sand, and coarse sand in the top one metre of the mineral soil).

Methods

A great variety of equations have been used to describe plant growth. Among the most popular are the Gompertz (1832), logistic (Verhulst, 1845, 1847), mono-molecular (Mitscherlich, 1919), Bertalanffy (1957), and Chapman-Richards (Richards, 1959) equations. In contrast to the seeming diversity of growth models, the above equations can be reduced to entail only two opposing factors: the biological potential for unlimited growth and a reduction due to ageing and environmental constraints. Recognising that the equations are all specific cases of two different model forms that were equally successful in predicting tree growth, Zeide (1993) suggested an alternative form that predicted individual-tree growth from tree size (y):

$$\frac{dy}{dt} = a_0 \cdot y^{a_1} \cdot e^{a_2 y} \quad (\text{IV.1})$$

This extremely flexible compound power function was used earlier by Warren (1980) and Monserud (1986) for standardizing tree ring data.

Diameter growth was modelled using a difference equation form of Equation (IV.1), which was further expanded to include measures of competition. Two major forms of competition are often identified in crowded plant populations: one- and two-sided competition (Schwinning and Weiner, 1998). Competition for light is considered to be one-sided, because larger individuals shade smaller ones but the reverse seldom occurs. Conversely, competi-

tion for below-ground resources is considered two-sided as plants have equal access to those resources. Preliminary analyses of a series of different modifiers to describe the effect of competition on individual-tree growth showed that stand basal area (G) and the basal area of larger trees (G_L) were efficient in describing the one- and two-sided competition effects, respectively. Among the different models tested in this study, the following model gave the best fit to the diameter data:

$$\frac{\Delta d_{i,t}}{\Delta t} = a_0 \cdot (d_{i,t} + k_1)^{a_1} \cdot e^{a_2 d_{i,t}} \cdot e^{a_3 G_t} \cdot e^{a_4 \frac{G_{L,i,t}}{\ln(d_{i,t} + k_2)}} + \varepsilon_{D,i,t} \quad (\text{IV.2})$$

where $d_{i,t}$ is diameter at breast height (mm) of the i th tree at time t , Δd_i is diameter increment (mm) of a one-year growth interval (Δt), G is basal area ($\text{m}^2 \text{ ha}^{-1}$), G_L is basal area of the trees larger than the subject tree ($\text{m}^2 \text{ ha}^{-1}$), $\varepsilon_{D,i,t} \sim N(0, \sigma_D^2)$ is the random error, and a_0 – a_4 are parameters to be estimated. Further, k_1 is a parameter estimated from data that allows growth for $d_{i,t} = 0$ and k_2 is a constant equal to 1 that ensures a positive denominator for small trees.

Ratkowsky (1983) found problems with intrinsic nonlinearity (IN curvature) and parameter effects curvature (PE) in sigmoid growth models. Although no remedy exists for IN curvature, problems with PE curvature may be reduced by a re-parameterisation of the model. Problems with PE curvature in models similar to Equation (IV.2) were encountered during the development of a growth simulator for the Pacific Northwest (ORGANON) (Hann and Larsen, 1991) and was reduced by an exponential re-parameterisation of the model (D.W. Hann, Oregon State University, personal communication, 2004). After re-parameterisation diameter growth was estimated as follows:

$$\begin{aligned} \frac{\Delta d_{i,t}}{\Delta t} = \exp & \left(a_0 + a_1 \cdot \ln(d_{i,t} + k_1) + a_2 \cdot d_{i,t} + \right. \\ & \left. + a_3 \cdot G_t + a_4 \cdot \frac{G_{L,i,t}}{\ln(d_{i,t} + k_2)} \right) + \varepsilon_{D,i,t} \end{aligned} \quad (\text{IV.3})$$

Similar models have been used for predicting growth of Douglas-fir and other conifer species (Wykoff, 1990; Ritchie and Hann, 1997; Bravo et al., 2001).

Height increment was estimated using a model form similar to Equation (IV.3). Modellers of individual-tree height growth have recognised that some measure of crown competition often provides a reliable modifier to potential height growth due to competition (Pretzsch et al., 2002; Hann et al., 2003). In the present study only a limited number of observations

on crown characteristics were obtained and more indirect measures of crown competition were used instead. Like in the diameter model, G_L and G were chosen to represent one- and two-sided competition, respectively. Further, the d/h -ratio was introduced to model the effect of tree vigour, as a substitute for crown ratio used by a number of authors (Daniels and Burkhardt, 1975; Ritchie and Hann, 1986):

$$\frac{\Delta h_{i,t}}{\Delta t} = \exp\left(b_0 + b_1 \cdot \ln(h_{i,t}) + b_2 \cdot h_{i,t} + b_3 \cdot \frac{d_{i,t}}{h_{i,t}} + b_4 \cdot G_t + b_5 \cdot \frac{G_{L,i,t}^2}{\ln(d_{i,t})}\right) + \varepsilon_{H,i,t} \quad (\text{IV.4})$$

where Δh_i is diameter increment (dm), $h_{i,t}$ is total tree height (dm) of the i th tree at time t , $\varepsilon_{H,i,t} \sim N(0, \sigma_H^2)$ is the random error, and b_0 – b_5 are parameters to be estimated.

Mortality is often described using a nonlinear function bounded by 0 and 1, such as the logistic (Monserud, 1976; Johannsen, 1999; Monserud and Sterba, 1999; Flewelling and Monserud, 2002). The model should adequately describe that mortality rates are often high for very small trees, but rapidly decline, as the trees grow larger. Monserud and Sterba (1999) found that this effect was adequately described for a number of species, including beech, by the inverse breast height diameter.

As trees become very old the mortality rate is expected to increase again due to increasing senescence, causing a U-formed death-rate curve. This effect may be modelled by including terms of d and d^2 (Monserud and Sterba, 1999). Preliminary analyses of the mortality function revealed no significant effect of d or d^2 , presumably because the U-shaped form of mortality could not be observed because the oldest trees were only little more than 200 years old. Consequently, d and d^2 were left out of the mortality model.

Mortality usually increases with competition between trees. Competition may be described by a variety of stand density measures such as crown competition indices, G or G_L . In relation to mortality several authors have found that G_L is a useful measure of tree specific competition (Monserud and Sterba, 1999; Hann et al., 2003). This was supported by preliminary analyses and the logistic mortality model used in this study is then:

$$P_{i,t} = \left(1 + e^{c_0 + c_1 \cdot d_{i,t}^{-1} + c_2 \cdot G_{L,i,t}}\right)^{-1} \quad (\text{IV.5})$$

where $P_{i,t}$ is mortality probability of the i th tree at time t , and c_0 – c_2 are parameters to be estimated.

Model estimation

Because diameter and height increment and mortality were not measured annually the parameters of Equations (IV.3), (IV.4) and (IV.5) cannot be

estimated directly. Instead the difference equations may be written as a series of equations that increment growth or mortality probability from the initial observation to the end of the measurement cycle. Consider diameter increment, Equation (IV.3) may be written as:

$$\Delta d_{i,t} = f(d_{i,t}, G_t, G_{L,i,t}) + \varepsilon_{D,i,t} \quad (\text{IV.6.1})$$

$$\Delta d_{i,t+1} = f(d_{i,t} + \Delta d_{i,t}, G_{t+1}, G_{L,i,t+1}) + \varepsilon_{D,i,t+1} \quad (\text{IV.6.2})$$

\vdots

$$\Delta d_{i,t+j-1} = f(d_{i,t+j-1} + \Delta d_{i,t+j-1}, G_{t+j-1}, G_{L,i,t+j-1}) + \varepsilon_{D,i,t+j-1} \quad (\text{IV.6.j})$$

Summing the Equations (IV.6.1), (IV.6.2), ..., (IV.6.j) in accordance with Cao (2000) results in Equation (IV.7). Note that the model is estimated as the least squares estimator of the diameter at $t+j$ rather than the annual increment, where $d_{i,t+j}$ results from a numerical iteration.

$$d_{i,t+j} = \sum_{t=1}^j f(d_{i,t+j-1}, G_{t+j-1}, G_{L,i,t+j-1}) + d_{i,t} + \zeta_{D,i,t+j-1} \quad (\text{IV.7})$$

Interim values of G and G_L between measurements cannot be updated based on the predicted values of d as an intrinsic part of the estimation procedure. Instead Johannsen (1999) and Cao (2004) used a stand level model to continuously update values of G . However, this approach is not possible for G_L and hence an iterative approach was adopted in this study:

1. Diameters at the beginning of each growth period were used to calculate G and G_L , which were then used as prior estimates of interim values between measurements of these values.
2. The diameter growth Equation (IV.3) was estimated based on the present estimate of interim values of G and G_L .
3. Parameter estimates of the diameter growth equation were subsequently used to calculate new interim values of d and, subsequently, G and G_L .
4. The procedure was repeated from step 2 until convergence.

A special problem occurs with mortality as we have no knowledge on when the individual tree died during the measurement interval. Hence, the effect of mortality on interim values of G and G_L is not possible to quantify. This problem was handled by placing mortality at the end of the growth period (i.e. mortality during the measurement interval has no effect

on interim estimates of G and G_L). This was done because mortality is limited in the majority of the stands included in this study as most stands are thinned frequently. Hence, this assumption has only limited effect on interim values of G and G_L and is thus expected to have only minimal effect on the estimates of the diameter increment model.

The dichotomous nature of mortality (either a tree is dead or it is not) requires that the model is estimated by multivariate maximum likelihood or weighted nonlinear regression (Monserud and Sterba, 1999; Flewelling and Monserud, 2002). The annual mortality equation was estimated by continuously updating the survival probability from the initial observation to the end of the measurement cycle. When the error term is defined as $\varepsilon_{M,i} = Z_i - Z_i^*$, where Z_i^* is 0 and Z_i is defined in Equation (IV.8), minimising the squared errors leads to maximisation of the log-likelihood.

$$Z_i = \begin{cases} \sqrt{-2 \cdot \ln(P_{live,i,t+q})} & \text{-if tree } i \text{ is alive at the end of the period} \\ \sqrt{-2 \cdot \ln(1 - P_{live,i,t+q})} & \text{-if tree } i \text{ is dead at the end of the period} \end{cases} \quad (\text{IV.8})$$

where:

$$\begin{aligned} P_{live,i,t+q} &= \prod_{j=1}^q P_{live,i,t+j}, \\ P_{live,i,t+j} &= P_{live,i,t+j-1} \cdot (1 - P_{i,t+j}) \\ P_{live,i,t} &= 1 \end{aligned}$$

where $P_{live,i,t+q}$ is the survival probability at the end of the measurement interval $(t+q)$ of the i th tree and P_i is the mortality probability as defined in Equation (IV.5).

Parameter estimates of the height and mortality functions were determined using the estimated parameters of the diameter increment model (IV.3) to estimate interim values of d and G_L .

Error structure

Due to correlated error components, systems of equations such as the one presented here may not yield theoretically sound estimators (Borders, 1989). Other authors have recognised the relationship between diameter and height equations and used seemingly unrelated regression (SUR) to estimate the parameters in similar systems of equations (Johannsen, 1999; Cao, 2004). However, the effect of error correlations between different model components depends on the degree of correlation. If no error correlations exist, the regressions may be treated as independent estimation problems. If the

error correlation is small, the improvement resulting when including error correlations may very well be outweighed by the loss of data that occurs because heights are measured more infrequently than diameters. In this study, exclusion of all diameter measurements for which there were no height measurement (or vice versa) would have led to exclusion of about 9/10 of the available data. Further, an analysis of the error correlations between diameter and height increment models revealed no significant correlations between errors of the diameter and height models (coefficient of correlation = 0.08). It was therefore decided to treat the individual models as individual estimation problems.

It is generally recognised that repeated measures on individuals or samples are correlated, which often leads to error correlations and subsequently to inefficient estimates and underestimated standard errors when correlations are strong. In this study, serial correlations were modelled explicitly by a first-order autoregressive model that accommodates the irregular spacing of measurements:

$$\varepsilon_{m,j} = \rho_m^{t_j - t_{j-1}} \varepsilon_{m,j-1} + u_{m,j} \quad (i = 1, 2, \dots), \quad (\text{IV.9})$$

where $\varepsilon_{m,j}$ is the value of the j th error (i, t) and the m th equation, t is time in years, ρ_m is a parameter to be estimated for each equation and $u_{m,j} \sim N(0, \sigma^2)$ is the independently distributed random error.

Site-specific effects

In most studies of individual-tree growth site-specific effects have been related to some measure of site quality, most commonly site index (e.g., Hann et al., 2003). Johannsen (1999) found that the difference equation rate constant α_0 of the dominant height growth model (H_{100}) in Equation (IV.10) was closely related to site quality.

$$\frac{\Delta H_{100,t}}{\Delta t} = \alpha_0 \cdot H_{100,t}^{\alpha_1} \cdot e^{-\alpha_2 \cdot H_{100,t} + \alpha_3 \cdot G} \quad (\text{IV.10})$$

Johannsen (1999) related α_0 to the rate constants of individual-tree models for oak to model the effect of site quality on growth. In other studies, site-specific effects are modelled more directly, using abiotic variables such as soil characteristics, precipitation, elevation or slope (e.g. Wykoff, 1990; Pretzsch et al., 2002; Callesen, 2003).

In this study, parameters of the individual-tree diameter and height models were initially estimated globally except for the difference rate constants (a_0 and b_0 in Equation (IV.3) and (IV.4)), that were estimated locally for each experiment. This allows for testing the relation between the rate constants of the individual-tree models and different measures of site quality: *i*) site index, *ii*) α_0 of the dominant height growth model in Equation (IV.10),

and *iii*) the fraction of clay, silt, fine sand and coarse sand in the uppermost one metre of soil.

Preliminary analyses showed that the individual-tree difference equation rate constants (a_0 and b_0) were highly correlated with both site index (dominant height at base age 50 years) and the rate constants of the stand model (α_0 ; Equation (IV.10)). To allow calibration of the individual-tree model for different sources of input data, both individual diameter and height growth models were estimated after substituting the rate constant (a_0 or b_0 in Equation (IV.3) and (IV.4) respectively) with a function of site quality (either site index or α_0):

$$\begin{aligned} \frac{\Delta d_{i,t}}{\Delta t} = & \exp\left(a_{01} + a_{02} \cdot \ln(SQ) + a_1 \cdot \ln(d_{i,t} + k_1) + a_2 \cdot d_{i,t} + \right. \\ & \left. + a_3 \cdot G_t + a_4 \cdot \frac{G_{L,i,t}}{\ln(d_{i,t} + k_2)}\right) + \varepsilon_{D,i,t} \end{aligned} \quad (\text{IV.11})$$

$$\begin{aligned} \frac{\Delta h_{i,t}}{\Delta t} = & \exp\left(b_{01} + b_{02} \cdot \ln(SQ) + b_1 \cdot \ln(h_{i,t}) + b_2 \cdot h_{i,t} + \right. \\ & \left. + b_3 \cdot \frac{d_{i,t}}{h_{i,t}} + b_4 \cdot G_t + b_5 \cdot \frac{G_{L,i,t}^2}{\ln(d_{i,t})}\right) + \varepsilon_{H,i,t} \end{aligned} \quad (\text{IV.12})$$

where SQ is a measure of site quality (either site index or α_0 of the dominant height growth model) and a_{01} , a_{02} , $a_1 - a_4$, b_{01} , b_{02} , $b_1 - b_5$, and k_1 are global parameters to be estimated.

Model evaluation

The predictive performance on the model subject (i.e. annual growth rates and mortality) cannot be evaluated directly because annual growth rates and mortality are not known. Instead the subject for characterisation and assessment of errors is the periodic mean annual increment between measurements (PAI) rather than the predicted state of the model subject at the end of the period. The choice of evaluation criterion is motivated by the fact that the model estimated is an annual growth rate equation. Secondly, using the fit of the variable at the end of the period as the evaluation criterion leads to highly inflated estimates of fit statistics because much of the variation is explained by the initial state of the model subject.

Model error was first characterised in terms of magnitude and distribution by plotting residuals against predicted values as well as against tree and stand variables included in the models. Temporal and regional trends were evaluated by plots of residuals against measurement years and region according to Jakobsen (1976). In addition to the visual appraisal of the errors a number of summary statistics were calculated for the entire data as well as for different strata and initial values of the model subject. The

summary statistics include average bias (AB), average absolute bias (AAB), standard error of estimates (SEE), and root mean squared error (RMSE).

Statistical tests for appraisal of accuracy and precision of the model as well as the patterns and distribution of the residuals were carried out. The mortality model was evaluated by Akaike's information criterion (AIC; Akaike, 1976) as well as with χ^2 -statistics. The statistical tests of model bias of the diameter and height models included simultaneous F -tests for unit slope and zero intercept on the linear regression of observed versus predicted data (Dent and Blackie, 1979, p. 94–117). Tests of precision included R^2 -statistics, AIC and critical error confidence bounds (CEB) (Freese, 1960; Reynolds, 1984).

The predictive performance and extrapolation properties of the model were evaluated by a data-splitting procedure in which entire plots were randomly selected for either fitting or validation. The fit data was used to estimate the global regression coefficients. Based on these estimates, site-specific parameters of the models were estimated for the validation data. Model performance and extrapolation properties were evaluated by the RMSE of the evaluation data compared to the RMSE obtained from the fit data. Final parameter estimates were reported for the re-combined data to avoid an unacceptable loss of data.

Results

The signs of the parameter estimates of the diameter model (Table IV.2) confirm the assumption of diameter growth being a peaking function of d where $\Delta d \rightarrow 0$ as $d \rightarrow \infty$. Autocorrelation (ρ_D) was positive and highly significant. Annual diameter increment for an open-grown tree (calculated for a theoretical tree, where G_L in Equation (IV.3) is zero and G equals the basal area of one tree per hectare with diameter d_i) peaks at 34.3 cm regardless of site quality (Figure IV.1). Increasing values of both G and G_L cause a reduction in growth although the effect is greatest for G_L . The effect of G on annual diameter increment is independent of tree size whereas the effect of G_L is increasing with decreasing tree size.

The height growth model is a peaking function of h where $\Delta h \rightarrow 0$ as $h \rightarrow \infty$ as initially assumed (Table IV.2). Autocorrelation of the height growth model (ρ_H) was not significant ($P > 0.05$). Annual height increment for an open grown tree peaks at a height of about 10 metres (Figure IV.2). G_L has a negative effect on height growth whereas height growth increases for increasing levels of G .

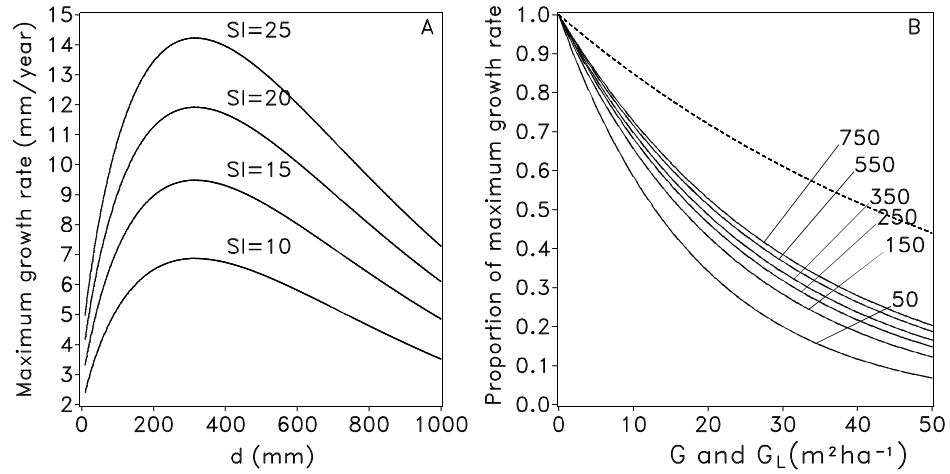


Figure IV.1: Annual diameter increment. (A) maximum growth at different levels of site index (Equation (IV.11)) for an open-grown tree. (B) the effect of G_L (full lines) and G (dashed line) for different levels of d (in mm).

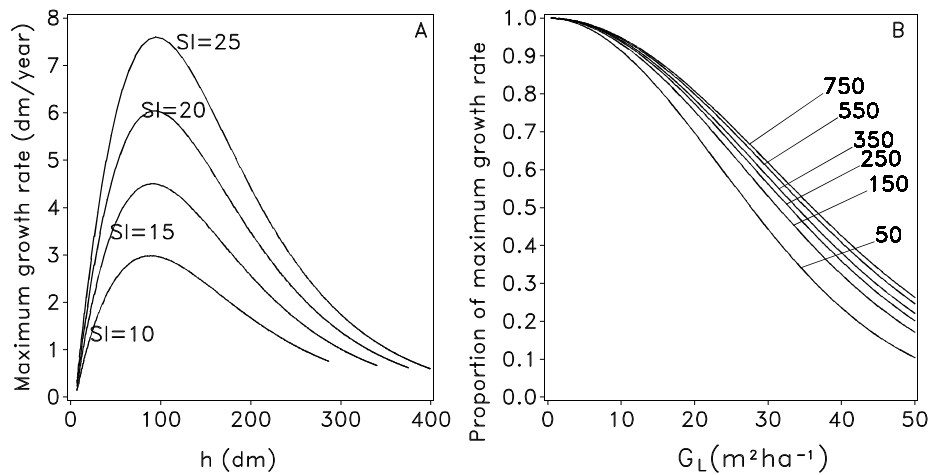


Figure IV.2: Annual height increment. (A) maximum growth at different levels of site index (Equation (IV.12)) for an open-grown tree. (B) the effect of G_L on height increment for different levels of d (in mm).

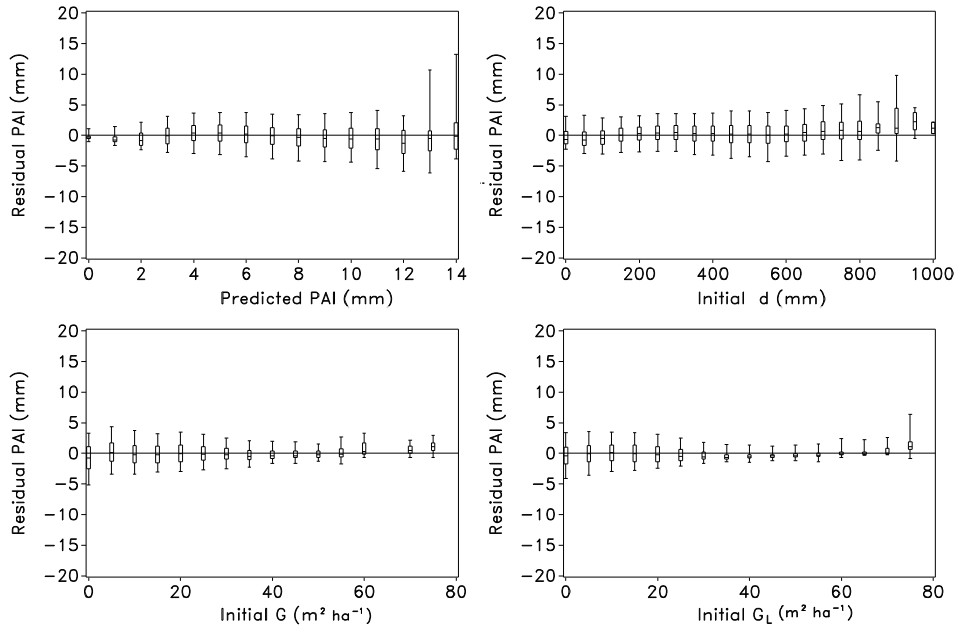


Figure IV.3: Box plots of residual PAI_d (observed minus predicted) versus predicted PAI_d and initial values of d , G and G_L . Boxes show the median and 25th and 75th percentiles. High and low bounds on the whiskers show 95th and 5th percentiles.

Parameter estimates of the mortality function (IV.5) indicate that mortality decreases with increasing diameter and tree size and increases with increasing competition, here modelled by G_L (Table IV.2).

Residuals of the diameter growth model were approximately normally distributed and showed no obvious bias when plotted against the independent variables (Figure IV.3), although it seems that the model may slightly underestimate the growth of very big trees. The latter finding is based on very few observations relative to the total dataset and may not be valid. Residuals were approximately homogeneous across diameter (Table IV.3), PAI , G , G_L , and the length of measurement intervals (not shown). The average bias confirms the apparent underestimation of diameter growth for trees larger than 65 cm, and simultaneous F-statistics show significant model bias ($P \leq 0.05$). The average absolute bias was 1.516 mm and the model explained little more than half the variation in PAI ($R^2 = 0.559$). The critical error confidence bounds (CEB) are 3.92-3.94 mm, which may seem relatively wide, considering that the average annual diameter growth is 4.14 mm. The data-splitting procedure resulted in only a small increase in RMSE (4.0%).

Residuals of the height growth model were approximately normally dis-

Table IV.2: Parameter estimates of diameter growth, height growth and mortality models. All parameters were highly significant ($P < 0.0001$) except for the estimate of autocorrelation of the height growth model ($P > 0.05$). Approximate standard errors are given in italics below parameter estimates.

Model	Parameters ^a							
	0	1	2	3	4	5	k_1	k_2 ρ
Diameter	-2.2864 ^b	0.9700	-0.0026	-0.0183	-0.2007		25.6174	1 0.8596
	<i>0.1233^b</i>	<i>0.0224</i>	<i>5.2E-5</i>	<i>2.44E-4</i>	<i>0.0011</i>		<i>1.9325</i>	<i>0.0011</i>
Height	-5.1608 ^b	1.7589	-0.0179	0.2769	0.0111	-0.0028		NS
	<i>0.2312^b</i>	<i>0.0521</i>	<i>3.63E-4</i>	<i>0.0237</i>	<i>7.14E-4</i>	<i>1.25E-4</i>		.
Mortality	7.4247	-36.7827	-0.0876					
	<i>0.0204</i>	<i>0.3176</i>	<i>5.44E-4</i>					

^anumbers refer to parameter suffix in Equation (IV.3), (IV.4), and (IV.5)
^bEstimated individually for each experiment, number represents a simple average.

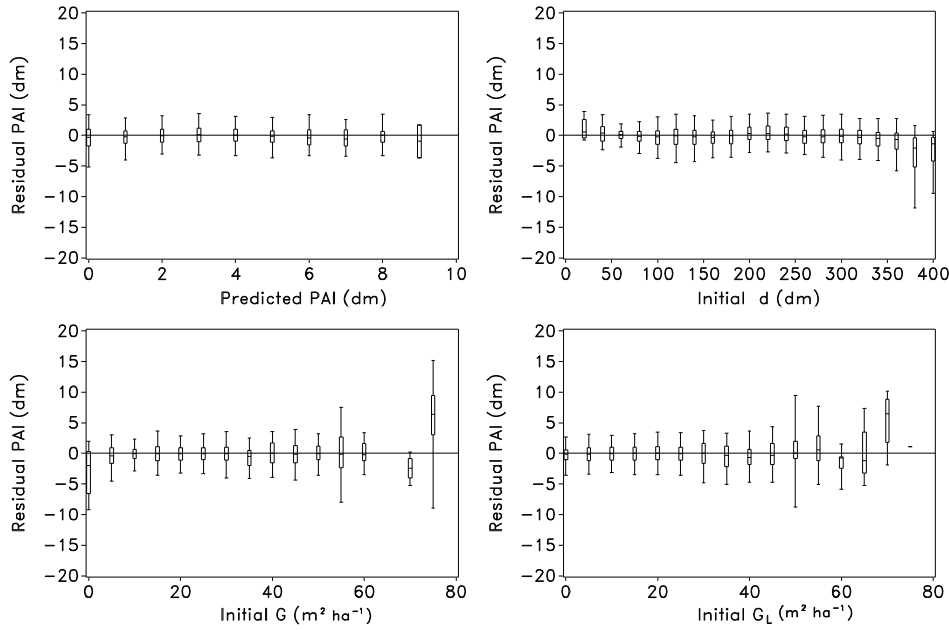


Figure IV.4: Box plots of residual PAI_h (observed minus predicted) versus predicted PAI_h and initial values of h , G and G_L . Boxes show the median and 25th and 75th percentiles. High and low bounds on the whiskers show 95th and 5th percentiles.

tributed and showed no obvious bias when plotted against the independent variables, except for very tall trees where the model apparently overestimates growth (Figure IV.4). This bias was reflected in the simultaneous F-statistics that showed an overall bias of the model ($P \leq 0.05$). Residuals were approximately homogeneous across diameter (Table IV.3), PAI , G , G_L , and the length of measurement intervals (not shown). The average absolute bias of the height growth model is 1.504 dm and the model explained only a little more than one third of the variation in PAI ($R^2 = 0.370$). The latter may be explained by the inherent difficulties in measuring height on live trees, which in turn also explains the increasing variation with increasing size of the trees. The critical error confidence bounds (CEB) are 4.24-4.31 dm, which again seem relatively large, when considering the average annual height increment of 2.91 dm.

The rate constants of the diameter and height growth functions were related to soil texture variables of the uppermost one metre of the soil on 48 experiments (Figure IV.5). The relation between the rate constant and fractions of clay, silt, fine sand or coarse sand was not significant ($P \geq 0.05$), dismissing the hypothesis that the rate constant is directly linked to a simple set of soil characteristics.

Table IV.3: Fit statistics of the diameter and height increment models. Root mean square error (RMSE), average bias (AB) and standard error of the estimates (SEE) in millimetres by diameter class. Frequency refers to the number of pairwise observations of diameter and height at the beginning and end of the period, used in the estimation of the model.

d cm	Diameter model					Height model				
	Freq	RMSE	Bias	SEE		Freq	RMSE	Bias	SEE	
		mm	mm	mm			dm	dm	dm	dm
All	193614	2.00	-0.03	2.00		19947	2.18	-0.11	2.19	
0-5	21246	1.96	-0.33	1.96		707	1.50	0.12	1.59	
5-10	48638	1.98	-0.44	1.98		1959	2.14	-0.42	2.18	
10-15	38229	1.86	-0.09	1.87		2685	2.26	-0.24	2.29	
15-20	25603	1.89	0.24	1.89		2741	2.21	-0.06	2.24	
20-25	15345	1.99	0.36	1.99		2464	2.01	0.10	2.05	
25-30	9944	2.03	0.53	2.04		1973	1.97	0.27	2.01	
30-35	8037	2.04	0.32	2.05		1726	2.21	0.09	2.26	
35-40	7436	2.10	0.32	2.11		1559	2.23	-0.04	2.29	
40-45	7024	2.32	0.26	2.34		1166	2.22	-0.12	2.29	
45-50	5281	2.42	0.20	2.44		827	2.17	-0.06	2.28	
50-55	3168	2.42	0.13	2.45		675	2.20	-0.40	2.34	
55-60	1782	2.59	0.10	2.64		526	2.58	-0.67	2.78	
60-65	908	2.47	0.37	2.58		383	2.45	-0.64	2.73	
65-70	490	2.72	0.72	2.96		231	3.05	-0.75	3.71	
70-75	228	2.88	0.77	3.51		141	3.15	-0.86	4.60	
>75	255	3.20	1.01	3.80		184	2.68	-0.39	3.48	

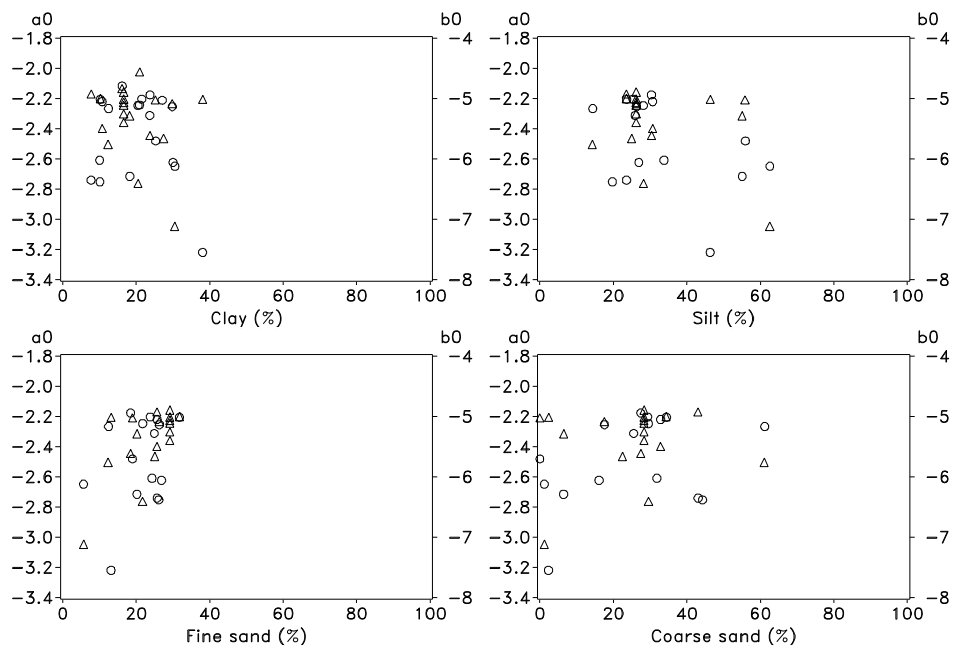


Figure IV.5: Plots of difference equation rate constants for the diameter (a_0 , circles) and height (b_0 , triangles) models plotted against soil fractions in the top one metre soil.

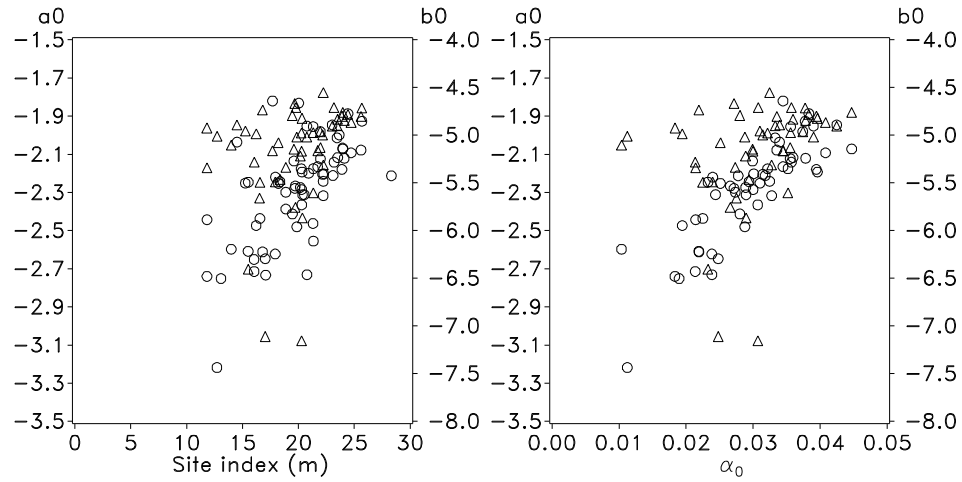


Figure IV.6: Plots of difference equation rate constants for the diameter (a_0 , circles) and height (b_0 , triangles) models plotted against site index and the difference equation rate constant (α_0) of the dominant height growth model (Equation (IV.10)).

The rate constants of both the individual-tree diameter and height growth functions (a_0 and b_0) was related to both site index (dominant height at base age 50 years) and the rate constant of the stand model (α_0 ; Equation (IV.10)). The relation was highly significant for both models ($P < 0.0001$), which indicated that both site index and α_0 may be used as indicators of site quality in predicting individual-tree growth (Figure IV.6). Parameter estimates of the individual-tree models estimated with site index (SI) and α_0 as indicators of site quality (Equation (IV.11) and (IV.12)) are provided in Table IV.4. The estimation resulted in a slightly worse fit than when the model was estimated individually for each plot.

Discussion and conclusions

The iterative method applied for estimating the difference equations converged after just few iterations (< 10) once the initial parameter guesses were sufficiently close to the parameter estimates. As such, the method proved to be adequate for data having irregular measurement intervals. The use of various indicators of site quality allows for a variety of different uses of the estimated models. If sufficient individual-tree data are available e.g., from research plots, a_0 or b_0 in Equation (IV.3) and (IV.4) may be estimated directly and used for simulation studies. Otherwise individual-tree growth may be estimated based on an estimate of α_0 from a series of dominant height measurements or from an estimate of site index. However, based

Table IV.4: Parameter estimates of the diameter and height growth models for different indicators of site quality (ISQ): Site index (SI) and α_0 (Equation (IV.10)). All parameters were highly significant ($P < 0.0001$) except for those marked "NS" ($P > 0.05$).

Model	ISQ	Parameters ^a									
		01	02	1	2	3	4	5	k_1	k_2	ρ
Diameter	SI	-3.4642 <i>0.1152</i>	0.7938 <i>0.0073</i>	0.7281 <i>0.0213</i>	-0.0021 <i>5.0E-5</i>	-0.0164 <i>1.98E-4</i>	-0.2109 <i>0.0011</i>		22.5321 <i>2.4180</i>	1	0.8757 <i>0.0010</i>
Height	SI	-7.5407 <i>0.1926</i>	1.1324 <i>0.0292</i>	1.5513 <i>0.0444</i>	-0.0163 <i>2.97E-4</i>	0.1563 <i>0.0205</i>	0.0138 <i>6.18E-4</i>	-0.0035 <i>1.27E-4</i>			NS
Mortality	SI	7.4157 <i>0.0204</i>	-36.2820 <i>0.3159</i>	-0.0875 <i>5.44E-4</i>							.
Diameter	α_0	0.8210 <i>0.0250</i>	0.5381 <i>0.0044</i>	0.7449 <i>0.0053</i>	-0.0021 <i>2.2E-5</i>	-0.0230 <i>2.04E-4</i>	-0.1916 <i>0.0011</i>		NS	1	0.8649 <i>0.0011</i>
Height	α_0	-1.1753 <i>0.1851</i>	0.9873 <i>0.0225</i>	1.6745 <i>0.0421</i>	-0.0166 <i>2.84E-4</i>	0.1724 <i>0.0196</i>	0.0100 <i>6.20E-4</i>	-0.0033 <i>1.25E-4</i>			NS
Mortality	α_0	7.5311 <i>0.0212</i>	-49.7868 <i>0.3707</i>	-0.0877 <i>5.51E-4</i>							.

Notes:

Diameter model (SI): AAB: 1.575 mm; R^2 : 0.525; R^2 without bias: 0.525; CEB: 4.061-4.083 mm

Height model (SI): AAB: 1.544; R^2 : 0.348; R^2 without bias: 0.350; CEB: 4.332-4.404 dm

Diameter model (α_0): AAB: 1.523 mm; R^2 : 0.546; R^2 without bias: 0.547; CEB: 3.953-3.974 mm

Height model (α_0): AAB: 1.538; R^2 : 0.352; R^2 without bias: 0.357; CEB: 4.317-4.389 dm

^anumbers refer to parameter suffix in Equation (IV.11), (IV.12), and (IV.5)

on the findings of this study, individual-tree growth cannot be estimated from soil characteristics alone. This finding is in concordance with Callesen (2003), who did not find a significant relation between the height growth rate of beech in 14 Danish permanent sample plots and any single soil texture class. Lack of correlation between soil properties and indicators of site quality were also observed by Leary et al. (1997), whereas Carbonnier (1975) and Johannsen (1999) observed positive correlations between tree growth and sand/silt contents of the soil for Sweden and Denmark.

The system of individual-tree models overall conformed to the expected behaviour of tree growth and mortality. G_L has a negative effect on diameter and height growth (Figures IV.1 and IV.2), presumably caused by increasing competition. The effect of G_L on diameter and height increment increases with decreasing tree size, indicating that G_L expresses one-sided competition for light (i.e. that large trees have disproportionate access to the contested resource) as initially assumed. Stand basal area (G) has a negative effect on diameter growth. The effect is independent of tree size, which is concordant with the assumption of G as an expression of two-sided competition for below-ground resources. G apparently has a different effect on height growth than observed for diameter growth as parameter estimates indicate an increasing height growth with increasing G . This effect is probably due to the effect of stand density on intra tree allocation, because trees that grow in denser stands allocate more resources to height growth than open-grown trees. As also expected, the effect of the d/h -ratio is positive, indicating that trees with relatively thick stems grow better. This effect may be attributed to the fact that trees with larger crowns and thereby a larger potential for growth tend to have thicker stems.

Current annual diameter increment for an open grown tree peaks independently of site quality (Figure IV.1 and IV.2). This is an artefact of the model form as differentiating the growth model in Equation (IV.3) for $G_L = 0$ with respect to d , setting the growth acceleration equal to 0 and solving for d gives $d_{max} = \frac{-a_1}{a_2} - k_1$. This property of the selected model may be dubious from a biological point of view as we might expect the location of the peak to depend on site quality (Brunner et al., 2006). This proposition was tested by modelling a_2 in Equation (IV.3) as a linear function of the site-specific parameter. The slope parameter of this function was significant and signs of parameter estimates indicated that peak growth occurred earlier on good sites than on less good. However, the effect of the site specific parameter on the location of the peak was limited (± 1 cm), and the extra parameter had little effect on model predictions, which is why the effect was omitted in the final equation.

A thinning effect apart from the mere effect of the change in G and G_L , the so-called release effects or "lichtungszuwachs" (Freist, 1962) has been modelled by other authors (Hann and Hanus, 2002a,b). In this study, release effects were modelled by discounting the effect of the proportion of

basal area removed in previous thinnings, using a similar approach as Hann and Hanus (2002a). A significant but very small effect limited to the first year after the thinning was observed. The limited effect may be due to the regime of frequent, light thinnings, which was not sufficient for expression of the release effects. Because of the limited effect on model predictions and the added model complexity, explicit modelling of the release effect was omitted in the final model.

Both diameter and height models showed significant model bias although the systematic deviations from the observed mean were relatively small. The bias of the height growth model was probably caused by increasing senescence and top dying, which caused the trees to 'grow' downward. The model form cannot handle this effect and it is questionable whether it should. Precision of the growth models may be regarded as weak given the large variance relative to the size of annual growth. However, Holmsgaard (1955) found large variations of annual growth in beech and attributed the variation to the precipitation during the growing season and in the previous year. Wichmann (2002) supported these findings and argued that essentially the competition symmetry is influenced by the precipitation during the present and previous three growing seasons. He further argued that this explains for the rather small improvements in predictive capability gained by increasingly complex models. As such, the observed lack of precision is expected when considering that the average measurement interval is only 3.8 years and may not be mitigated unless meteorological data are included.

Acknowledgements

I gratefully acknowledge the many constructive suggestions made by Vivian Kvist Johannsen, Henrik Meilby and Jens Peter Skovsgaard. Furthermore, I owe a dept of gratitude to Professor David W. Hann for his inspiration and Oregon State University for hosting me during the making of this study. The study was funded by Danish Forest & Landscape Research Institute, Danish Forest and Nature Agency and Danish Agricultural and Veterinary Research Council. Data was provided by *Forest & Landscape*, Royal Veterinary and Agricultural University.

Literature cited

Akaike, H. (1976). Canonical correlation analysis of time series and the use of an information criterion. In Mehra, R. K. and Lainotis, D. G., editors, *System identification: Advances and case studies*, pages 52–107. Academic Press, New York. 593 p.

- Bertalanffy, L. v. (1957). Quantative laws in metabolism and growth. *Quart. Rev. Biol.*, 32:217–231.
- Borders, B. E. (1989). Systems of equations in forest stand modelling. *For. Sci.*, 35:548–556.
- Bravo, F., Hann, D. W., and Maguire, D. A. (2001). Ipmpact of competitor species composition on predicting diameter growth and survival rates of Douglas-fir trees in southwestern Oregon. *Can. J. For. Res.*, 31:2237–2247.
- Brunner, A., Hahn, K., Biber, P., and Skovsgaard, J. P. (2006). Conversion of Norway spruce: A case study in Denmark based on silvicultural scenario modelling. In Hasenauer, H., editor, *Sustainable Forest Management – Growth Models for Europe*, pages 343–372. Springer, Berlin, Heidelberg, New York. 389 p.
- Callesen, I. (2003). *Transfer functions for carbon sequestration, nitrogen retention and nutrient release capability in forest soils based on soil texture classification*. PhD thesis, Royal Veterinary and Agricultural University. Copenhagen, Denmark. 247 p.
- Cao, Q. V. (2000). Prediction of annual diameter growth and survival for individual trees from periodic measurements. *For. Sci.*, 46:127–131.
- Cao, Q. V. (2004). Annual tree growth predictions from periodic measurements. Gen. Tech. Rep. SRS-71, U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC. 600 p.
- Carbonnier, C. (1975). Produktion i kulturbestånd av ek i Södra Sverige. *Studia Forestalia Suecica*, 125:1–89.
- Clutter, J. L. (1963). Compatible growth and yield models for loblolly pine. *For. Sci.*, 9:354–371.
- Daniels, R. and Burkhart, H. (1975). Simulation of individual tree growth and stand development in managed loblolly pine plantations. Technical Report FWS-5-75, Div. For. Wild. Res., Virginia Polytechnic and State University, Blacksburg, VA. 69 p.
- Dent, J. B. and Blackie, M. J. (1979). *Systems Simulation in Agriculture*, pages 94–117. Applied Science Publishers ltd., London. 180 p.
- Flewelling, J. W. and Monserud, R. A. (2002). Comparing methods for modelling tree mortality. In Crookston, N. L. and Havis, R. N., editors, *Proceedings of the Second forest vegetation simulator conference*, pages 168–175. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

-
- Freese, F. (1960). Testing accuracy. *For. Sci.*, 6:139–145.
- Freist, H. (1962). Untersuchungen über den Lichtungszuwachs der Rotbuche und seine Ausnutzung in Forstbetrieb. *Forstwissenschaftliches Centralblatt*, 17:1–78.
- Gompertz, B. (1832). On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Phil. Trans. Roy. Soc. London*, 123:513–585.
- Hann, D. W. and Hanus, M. L. (2002a). Enhanced diameter-growth-rate equations for undamaged and damaged trees in Southwest Oregon. Research Contribution 39, Forest Research Lab, College of Forestry, Oregon State University. 54 p.
- Hann, D. W. and Hanus, M. L. (2002b). Enhanced height-growth-rate equations for undamaged and damaged trees in Southwest Oregon. Research Contribution 41, Forest Research Lab, College of Forestry, Oregon State University. 38 p.
- Hann, D. W. and Larsen, D. R. (1991). Diameter growth equations for fourteen tree species in southwest Oregon. Research Bulletin 69, Forest Research Lab, College of Forestry, Oregon State University. 18 p.
- Hann, D. W., Marshal, D. D., and Hanus, M. L. (2003). Equations for predicting height-to-crownbase, 5-year diameter-growth rate, 5-year height-growth rate, 5-year mortality rate, and maximum size density trajectory for Douglas fir and western hemlock in the coastal region of the Pacific Northwest. Research Contribution 40, Forest Research Lab, College of Forestry, Oregon State University. 83 p.
- Holmsgaard, E. (1955). Årringsanalyser af danske skovtræer. *Det Forstlige Forsøgsvæsen i Danmark*, 22:1–246.
- Jakobsen, N. K. (1976). Natural-geographical regions of Denmark. *Geografisk Tidsskrift*, 75:1–7.
- Johannsen, V. K. (1999). *A growth model for oak in Denmark*. PhD thesis, Royal Veterinary and Agricultural University. Copenhagen, Denmark. 197 p.
- Leary, R., Nimerfro, K., Brand, M. H. G., Burk, T., Kolka, R., and Wolf, A. (1997). Height growth modelling using second order differential equations and the importance of initial height growth. *For. Ecol. Man.*, 97:165–172.
- McDill, M. E. and Amateis, R. E. (1993). Fitting discrete-time dynamic models having any time interval. *For. Sci.*, 39:499–519.

- Mitscherlich, E. A. (1919). *Landwirtschaftliche Jahrbücher*, 53:167–182.
- Monserud, R. A. (1976). Simulation of forest tree mortality. *For. Sci.*, 22:438–444.
- Monserud, R. A. (1986). Time-series analyses of tree ring chronologies. *For. Sci.*, 32:349–372.
- Monserud, R. A. and Sterba, H. (1999). Modelling individual tree mortality for Austrian forest species. *For. Ecol. Man.*, 113:109–123.
- Pretzsch, H., Biber, P., and Dürský, J. (2002). The single tree-based stand simulator SILVA: construction, application and evaluation. *For. Ecol. Man.*, 162:3–21.
- Ratkowsky, S. A. (1983). *Nonlinear regression modelling*. Marcel Dekker, New York. 276 p.
- Reynolds, M. R. (1984). Estimating the error in model predictions. *For. Sci.*, 30:454–469.
- Richards, F. J. (1959). A flexible growth equation for empirical use. *Journal of Experimental Botany*, 10:290–300.
- Ritchie, M. W. and Hann, D. W. (1986). Development of a tree height growth model for Douglas-fir. *For. Ecol. Man.*, 15:135–145.
- Ritchie, M. W. and Hann, D. W. (1997). Evaluation of individual-tree and disaggregative prediction methods for Douglas-fir stands in western Oregon. *Can. J. For. Res.*, 27:207–216.
- Schwinning, S. and Weiner, J. (1998). Mechanisms determining the degree of size-asymmetry in competition among plants. *Oecologia*, 113:447–455.
- Verhulst, P. F. (1845). Recherches mathématiques sur la loi d'accroissement de la population. *Nouv. mém. de l'Academie Royale des Sci. et Belles-Lettres de Bruxelles*, 18:1–41.
- Verhulst, P. F. (1847). Deuxième mémoire sur la loi d'accroissement de la population. *Mém. de l'Academie Royale des Sci., des Lettres et des Beaux-Arts de Belgique*, 20:1–32.
- Warren, W. G. (1980). On removing the growth trend from dendrochronological data. *Tree Ring Bull.*, 40:35–44.
- Wichmann, L. (2002). *Modelling the effects of competition between individual trees in forest stands*. PhD thesis, Royal Veterinary and Agricultural University. Copenhagen, Denmark. 112 p.

- Wykoff, W. R. (1990). A basal area increment model for individual conifers in the northern Rocky Mountains. *For. Sci.*, 36:1077–1104.
- Zeide, B. (1993). Analysis of growth equations. *For. Sci.*, 39:594–616.

Paper V

Quantifying size-asymmetric
growth

Quantifying size-asymmetric growth among individual beech trees

Thomas Nord-Larsen ^{*1}, Christian Damgaard[†], and Jacob Weiner[‡]

^{*}Royal Veterinary and Agricultural University, Forest & Landscape,
Hørsholm Kongevej 11, DK-2970 Hørsholm, Denmark, e-mail address:
tnl@kvl.dk

[†]Department of Terrestrial Ecology, National Environmental Research
Institute, Vejlesøvej 25, DK-8600 Silkeborg, Denmark, e-mail address:
cfd@dmu.dk

[‡]Royal Veterinary and Agricultural University, Department of Ecology,
Rolighedsvej 21, DK-1958 Frederiksberg, Denmark, e-mail address:
jw@kvl.dk

Abstract

We modelled the growth of individual trees in populations of European beech grown under different thinning regimes with a modified Richards equation. The effect of competition on growth was modelled by coupling the n individual equations simultaneously with a saturation term. By assuming that the growth of an individual within the population is a function of its size to a power a , a measure of the growth advantage of larger individuals (size-asymmetric growth) is provided. If $a > 1$, larger trees have a disproportionate advantage in growth and by inference, competition.

The degree of size-asymmetric growth, a , exceeded 1 in stands with large size variability and increased significantly at increasing density. This suggests that the predominant mode of competition is size-asymmetric and that this size-asymmetry increases with density. A measure of growth asymmetry is more informative than static measures of size inequality in understanding the growth dynamics of managed forest stands. Since a provides a measure of the relative importance of above- versus belowground competition, it may be useful in interpreting the growth dynamics of forest stands, and may provide an additional level of information for modellers of forest growth.

Keywords: Size-asymmetric competition, resources, pre-emption, depletion, Richards growth model

¹Corresponding author. Phone (+45) 35281758, Fax (+45) 35281517

Introduction

Growth of forest trees depends on their ability to compete for potentially limiting resources such as moisture, nutrients and light. The partitioning of a resource for which neighbouring individuals compete depends on the type of resource and whether the competition is mediated by depletion or by pre-emption of the resource. Completely symmetric competition occurs when contested resources are divided equally between competitors irrespective of their size, whereas size-symmetric competition occurs when uptake of contested resources is proportional to size. Similarly, completely asymmetric competition is a one-sided interaction in which the few largest individuals receive all contested resources leaving nothing for their smaller competitors (Schwinning and Weiner, 1998). In forest stands, competition among individual trees involves competition for several resources where competition for the individual resource is more or less prominent. The resulting interaction is somewhere on a continuum in which completely symmetric and completely asymmetric competition are the extremes.

Light is the primary example of a pre-emptable resource that generates size-asymmetric competition (i.e. larger individuals obtain a disproportionate share of contested resources; Schwinning and Weiner, 1998). In crowded populations, large individuals intercept most of the light, causing a steep vertical gradient of resource availability (Schwinning, 1996). The suppression of smaller individuals caused by size-asymmetric competition for light is considered to be the driving force in mortality and size inequality in crowded populations (Schwinning and Fox, 1995). Competition for below ground resources, on the other hand, appears to be size-symmetric (i.e. contested resources are divided in proportion to competitor size; Casper and Jackson, 1997; Weiner et al., 1997).

Although the underlying mechanisms of competitive interference between individual plants are difficult to investigate directly, we can observe the resultant growth patterns of individuals. If competition is intense and size-asymmetric, larger individuals receive more resources relative to their sizes, suppressing the growth of smaller individuals, such that larger individuals have higher relative growth rates than smaller individuals (size-asymmetric growth). This results in increasing size inequality (in the absence of significant density dependent mortality; Weiner, 1990). Thus, if competition is size-asymmetric, plants grown in dense populations should exhibit greater size inequality than plants growing at lower densities. If competition in dense populations is size-symmetric, size variability should be unchanged or lower at higher densities.

Models of individual tree growth that include the effects of competition have a long tradition in forest growth and yield modelling (see Vanclay, 1994, for numerous references). Most of these efforts have aimed to describe individual tree growth over a time interval as a function of plant size across the

population (McDill and Amateis, 1993). This approach has been criticized because each plant and time interval is treated separately and because the dynamic interactions among individuals are not modelled explicitly (Weiner et al., 1998). Coupling growth equations of individual plants allows for explicit modelling of these interactions and may help us build more biologically meaningful equations, because we can observe the effect of factors or treatments on parameters that can have clear biological interpretations (Damgaard, 1999). Coupled differential equations have been used to estimate the degree of size-asymmetric growth in monocultures of herbaceous plants at varying densities (Damgaard, 1999; Damgaard et al., 2002).

In this study we model individual tree growth with coupled differential equations to describe the dynamic nature of competition among trees. We use this approach to address the following questions:

1. Can coupled equations provide reasonable models for describing forest stand and individual tree growth?
2. What is the degree of size-asymmetric growth in beech stands grown at various densities?
3. How do thinning practices affect the degree of size-asymmetric growth?

Materials and methods

Data collection

Data originate from the permanent experiment DQ at Bregentved forest district in south east Denmark located at UTM-coordinates, European Datum 1950, zone 32: E695747 m, N6136389 m, 18 m above sea level. The parent material is morranic till from the Weichel glaciation having high clay content and a good nutrient supply, representing excellent growing conditions for European beech (*Fagus sylvatica* L.) in Denmark. The experiment is located in a beech stand established by strip sowing in 1916 and the sample plot structure was established in 1941. At the initiation of the experiment in 1941 the stand appeared quite uniform and the initial spacing of the individual plots was similar, although not identical (Holmsgaard, 1985).

The experiment comprises 11 individual sample plots with an area of 0.08 – 0.35 ha. Two of the sample plots are unthinned controls and the remaining plots were thinned according to two different thinning strategies named after their proponents: Jagd and Bavngaard (Holmsgaard, 1985). Jagd advocated early, heavy thinnings to achieve a rapid diameter growth and early financial returns, whereas Bavngaard advocated moderate thinnings at young ages and retention of understorey trees to achieve longer bole lengths and higher wood quality. The two thinning strategies lead to quite different stand structures where the plots thinned according to the ideas

of Jagd is more homogeneous in size than those thinned according to the ideas of Bavngaard. To reduce the computational load, 4 of the 11 plots were used in the estimation (A1, (Bavngaard), B2 (Jagd), C1 (Jagd) and E2 (unthinned control)). The four plots were chosen to represent the entire range of stand densities.

The plots were measured at every thinning, 11-13 times from 1941 to 1998, the total dataset comprising 136 individual measurement occasions. From 1941 to 1950 diameters were recorded in tally lists to 1-cm diameter classes. From 1953 all trees were numbered, marked permanently at breast height (1.3 m) and recorded individually, although understorey trees were still recorded in tally lists. Hence, from 1953 most of the individual trees are positively identifiable in subsequent years and this data was used for the analysis of individual tree growth in this study.

Observations of diameter are obtained by two sets of perpendicular caliper readings at breast height for each tree. The average of the two measurements is used as a measure of breast height diameter. Whether the tree is alive or dead at the time of measurement was also recorded. The total data comprises 24,843 diameter measurements of 3,530 individual trees. Individual tree height of living trees was obtained by a hypsometer, and felled trees were measured on the ground using a tape measure. The database comprises 3,949 height measurements on 1,538 individual trees.

Based on the paired observations of diameter and height, height-diameter equations were developed for each plot and measurement combination using a modified Näslund-equation (Näslund, 1936; Johannsen, 2002):

$$h = 1.3 + \left(\frac{d}{\alpha + \beta \cdot d} \right)^3 \quad (\text{V.1})$$

where d is the diameter at breast height, h is the total tree height and α and β are parameters to be estimated. The equations were then used to estimate the height of trees not measured. Individual tree volume was subsequently calculated for each individual tree based on a volume equation for beech (Madsen, 1987).

The four plots used in the analysis represent a wide range of stand densities expressed by stand basal area (G), obtained by summation of the cross sectional areas of the individual stems per hectare, and relative spacing ($RS = \left(\sqrt{10000/N} \right) / H$, where N is the number of stems per hectare and H is dominant height measured as the average height of the 100 thickest trees per hectare) (Figure V.1).

Model description

The choice of scalar measure of growth is not a trivial one as tree size represents a multidimensional vector and exhibits a high degree of plasticity

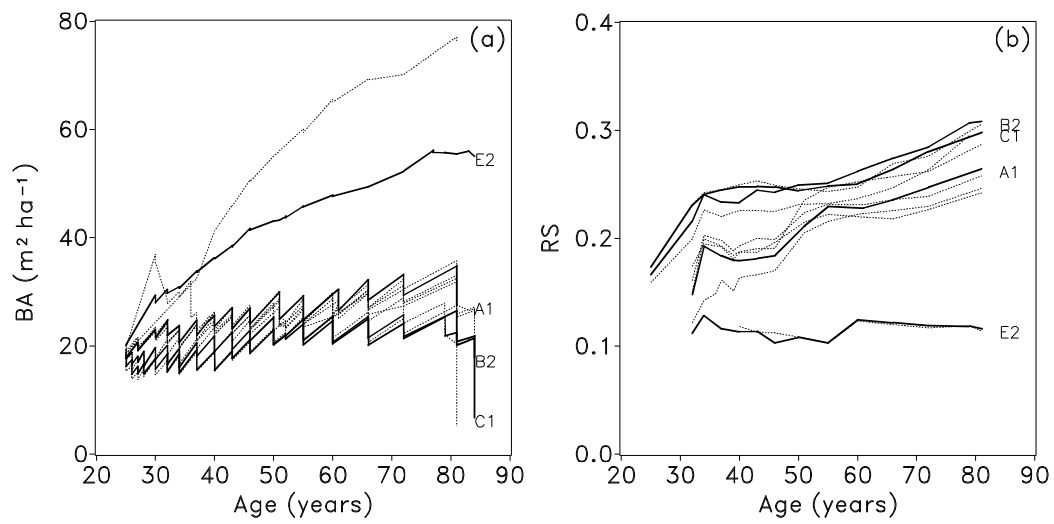


Figure V.1: Basal area (a) and relative spacing (b) for the 11 sample plots at experiment DQ. The four plots used in the analysis, A1 (Bavngaard), B2 (Jagd), C1 (Jagd) and E2 (unthinned control), are represented by the full black lines whereas the other plots are presented by dotted lines. The vertical drops in basal area represent the basal area removed in individual thinnings.

under different conditions. For each of the four plots we modelled both individual tree volume and basal area growth. This choice of scalar measures of size was dictated by available data that did not entail other measures of tree size, such as crown dimensions and we thus assumed that the amount of physiologically active tissue is correlated with volume and basal area.

We modelled individual tree growth by a modified Chapman-Richards growth model (Richards, 1959; Damgaard et al., 2002). The model has well known properties, is mathematically flexible and is among the most commonly used in modelling forest growth. The growth of n competitively interacting plants is modelled by n coupled differential equations, where the absolute growth rate is a function of tree size and a parameter accounting for the degree of asymmetric growth (a). The effect of competition between plants within the population is modelled by the cumulative size of the n individual trees relative to the fitted maximum cumulative size of the n trees ($n\alpha$):

$$\frac{dv_i(t)}{dt} = \begin{cases} \frac{\kappa}{1-\delta} f(v_i(t), a) \left(\left(\frac{1}{n\alpha} \sum_{j=1}^n v_j(t) \right)^{\delta-1} - 1 \right) & \delta \neq 1 \\ \kappa f(v_i(t), a) \left(\log(n\alpha) - \log \left(\sum_{j=1}^n v_j(t) \right) \right) & \delta = 1 \end{cases} \quad (\text{V.2})$$

for $t \geq 0$, $\kappa > 0$ and $\alpha > 0$. $v_i(t)$ is the size (volume or basal area) of tree i at time t , and κ , δ , and $f(v_i(t), a)$ determines the absolute growth rate of the tree. If $\delta > 0$, the growth curve is sigmoidal, and the slope of the tangent at the point of inflexion decreases with δ (Richards, 1959; Seber and Wild, 1989). α is the fitted maximum average tree size, and $n\alpha$ is the maximum cumulative size of the n competing trees. Thus, when the cumulative size reaches its maximum, reflecting maximum total biomass of the stand, growth stops.

The growth of individual trees is assumed to be proportional to a power function of their size (Schwinning and Fox, 1995; Damgaard, 1999; Wyszomirski et al., 1999):

$$f(v_i(t), a) = \begin{cases} 1 & a = 0 \\ v_i(t)^a & a > 0 \\ 1 \text{ (large plants) or } 0 \text{ (small plants)} & a = \infty \end{cases} \quad (\text{V.3})$$

where the effect of plant size on growth is quantified by the size-asymmetry parameter, a . If $a = 0$, all trees have the same growth rate irrespective of their size (i.e. growth is completely symmetric). If $0 < a < 1$, the growth rate is less than proportional to the size of the tree. If $a = 1$, the growth

rate is proportional to the size of the tree (i.e. growth is perfectly size-symmetric). If $a > 1$, the growth rate is more than proportional to the size of the tree and growth is size-asymmetric. If $a = \infty$, only the largest trees grow and growth is completely asymmetric.

Model estimation

In order to adequately describe the growth of a plant with a dimensionless size less than one the power function in Equation (V.3) was modified to $f(v_i(t), a) = (v_i(t) + 1)^a - 1$ since this is a monotonic increasing function of both size and the parameter a , for all $v_i(t) > 0$, while still passing through the origin (Damgaard, 1999). All parameters except for δ were exponentially reparameterized to ensure that they were strictly positive (all results are reported after parameter values have been transformed back). Both model and increment data was log-transformed to ensure homogeneity of variance. Trees that died or were thinned were only modelled until the time of death and hereafter assumed no longer to contribute to the population biomass (i.e. they no longer compete with living trees).

The coupled differential equations [Equation (V.2)] cannot be solved analytically, and the equations were solved numerically using the NDSolve routine of Mathematica (Wolfram, 2003). This routine simultaneously made incremental changes to the size of all trees at each measurement to the subsequent measurement for a specific parameter combination using sufficiently small steps. The likelihood of each parameter combination was then calculated from the transformed predicted increments and transformed observed increments for all n plants. The maximum likelihood estimates of the parameter values were found using the NMaximize routine of Mathematica (Wolfram, 2003).

The hypothesis of $a = 1$ was tested using a likelihood ratio test. The Bayesian posterior probability distributions of the parameters were calculated using the Metropolis-Hastings algorithm assuming an uninformative uniform prior distribution (100,000 samples with a burn-in period of 1000 iterations for stabilizing parameter values) (Carlin and Louis, 1996). Since the computational load increases rapidly with increasing number of trees, 100 randomly selected trees from each plot were used for calculating the posterior distributions. Statistical inferences were based on the 95% credibility intervals (2.5% - 97.5% percentile of the posterior distribution) of the parameters. Parameters were concluded to be significantly different if the 2.5% percentile of the high parameter was higher than the 97.5% percentile of the lower parameter.

The data used for this study represent a nested structure of repeated measurements on individual trees within different plots. Failure to recognize this correlation structure could result in inefficient estimates and underestimated standard errors when correlations are strong. However, both

within-plot correlations and the correlation of individual tree increments are generally not strong (Gertner, 1985; Reed and Burkhardt, 1985). Further, when growth as in this study is viewed as an incremental process where only current conditions affect current growth, the problems of serial correlation are generally avoided (García, 1983; Seber and Wild, 1989). Hence in this study we assumed that errors were uncorrelated but tested this assumption in the post hoc analysis.

Statistical fit of the model

Model assumptions were tested by visual inspection of residual plots and by statistical tests of homogeneity (Bartlett-Box test) and normality (Kolmogorov-Smirnov and Andersson-Darling tests) of residuals. Further, the hypothesis of no autoregression was tested by a Durbin-Watson test (Durbin and Watson, 1950):

$$d = \frac{\sum_{t=2}^n (e_t - e_{t-1})^2}{\sum_{t=1}^n e_t^2} \quad (\text{V.4})$$

where e_t is the residual at time t and d is the test statistic.

Statistical tests of model bias included simultaneous F -tests for unit slope and zero intercept on the linear regression of observed versus predicted data (Dent and Blackie, 1979):

$$F = \frac{(n_j - 2) \cdot \left(n_j a_j^2 + 2n_j \bar{X} a_j (b_j - 1) + \sum_{i=1}^{n_j} (X_i^2 (b_j - 1)^2) \right)}{2n_j MSE} \quad (\text{V.5})$$

where a_j and b_j is the intercept and slope of the regression of observed versus predicted values at the j th plot, X_i is the predicted values of the i th tree and MSE is the mean square error of the linear regression.

Precision of the model was evaluated by R^2 -statistics, the root mean square error (RMSE) and absolute average bias (AAB) of the back-transformed values.

Results

The Richards model accounted for more than 99% of the variation in the observed diameter and volume of the individual trees at the end of the measurement intervals (Table V.1). The model accounted for 81.2-92.2% of the observed diameter increment and 68.2-93.9% of observed volume increment

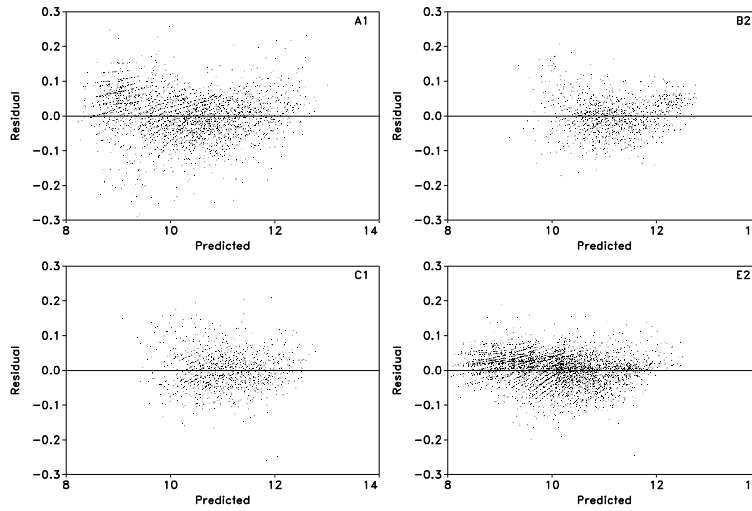


Figure V.2: Residual plot of untransformed residuals of diameter-square vs. the natural logarithm of predicted values (in mm) for the four plots.

(not shown). Residuals were approximately normally distributed with zero mean for all of the plots and variances were approximately homogeneous (Figure V.2). According to the simultaneous F-tests, the model was unbiased for both measures of size for plots B2 and C1. While the model was significantly biased for plots A1 and E2 for both measures of size, the bias was very small (Table V.1). Residuals were significantly correlated among individual trees, but correlations were small and did not affect model inferences adversely.

In heterogeneous stands, such as the control plots and in the plots subjected to the Bavngaard-regime, a exceeded 1, whereas a was less than 1 in the homogeneous stands of the Jagd-thinning regime (Table V.1). For both measures of tree size (basal area or estimated volume) a was significantly higher in the plots with higher densities (Control and Bavngaard) than in those of lower density (Jagd).

The 50% percentile of the posterior distributions of a were similar to the ML-estimate for most of the plots. However, in some cases the ML-estimate deviated significantly from the posterior distribution, which indicated that the estimation of the posterior distribution is somewhat sensitive to the selection of individual trees analyzed.

The posterior distributions of the other parameters of the sigmoid curve were also sampled. However, since diameter and volume growth are close to linear in the observed interval (Figure V.3), these parameters have a rather large credibility interval and are not very informative about the shape of the growth curves.

Table V.1: Maximum likelihood estimates of the parameter a in the growth model [Equation (V.2)]. All estimates of a were significantly different from 1 ($P < 0.0001$). The Bayesian posterior probability distributions of a based on a subsample of 100 trees are reported by the 2.5% percentile, 50% percentile and 97.5% percentile.

Measure	Regime	Plot	a	2.5%	50%	97.5%	R^2 ^a	RMSE ^a	AAB ^a
Diameter ²	Bavngaard	A1	1.4290	1.3699	1.4251	1.4919	0.994	7.621	4.772
	Jagd	B2	0.8333	0.6315	0.6776	0.7154	0.994	7.256	5.590
	Jagd	C1	0.9068	0.7707	0.8420	0.9018	0.993	7.377	5.257
	Control	E2	1.8900	1.8103	1.8645	1.9382	0.997	3.968	2.747
Volume	Bavngaard	A1	1.1979	0.0426	0.3497	0.6853	0.991	0.069	0.029
	Jagd	B2	0.6174	0.4459	0.7050	0.9113	0.995	0.064	0.040
	Jagd	C1	0.4609	0.2014	0.4076	0.5707	0.992	0.071	0.040
	Control	E2	2.4201	1.8904	2.1581	2.4018	0.985	0.043	0.023

^aBased upon back-transformed residuals of diameter and volume.

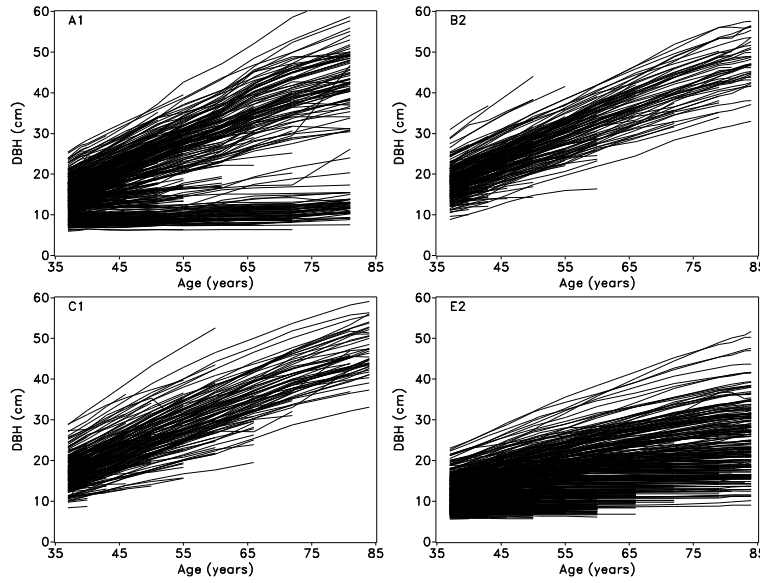


Figure V.3: Individual tree growth at plot A1 (Bavngaard), B2 (Jagd), C1 (Jagd) and E2 (unthinned control).

It may be argued that since the growth curves are almost linear a simpler growth model may be used to fit the parameter of interest, a , instead of a sigmoid growth model. We also fitted a simple saturation model, the monomolecular model ($\delta = 0$) to the data. In the cases where δ differed significantly from 0, the Richards model fitted better than the simpler model. In the other cases where δ of the Richards model was not significantly different from 0, the maximum likelihood estimates of a were almost identical (results not shown). As the choice of model in those cases apparently did not affect the estimates of the parameter of interest, a , the more flexible Richards growth model were used in the reported fitting procedures.

Discussion

Consistent with the previous studies showing that growth is size-asymmetric in crowded plant populations, a exceeded 1 in the control plots and in the plots subjected to the Bavngaard-regime. For both measures of tree size (basal area or estimated volume) a increased significantly with increasing stand density. Thus, our findings provide further evidence that the overall mode of competition between individual trees is size-asymmetric and that size-asymmetry of growth increases with population density, that is, the advantage of being larger is greater in more crowded populations.

In the more size homogeneous stands of the Jagd thinning regimes, a

was less than one. This may simply reflect a general inability to observe size-asymmetric growth in homogeneous stands (i.e. if all trees have the same size, size-asymmetric growth will not be observed, even if the underlying competitive process is size-asymmetric). Another possible explanation is that the Jagd thinning regime has an overall lower density and hence competition is expected to be more size-symmetric, although the differences in density between the two regimes are not very pronounced. Thinning will reduce the intensity of competition and therefore the degree of competitive asymmetry, but if the thinning regime increases size variation within the population it will increase the potential for size-asymmetric competition to result in size-asymmetric growth.

Our findings are consistent with those from a study on interspecies competition in cedar-hemlock forests in British Columbia. Using measures of relative height and distance-dependent competition indices, competition was found to be asymmetric and depended on neighbour identity (Simard and Sachs, 2004). Asymmetric competition has also been reported in numerous non-woody species including *Helianthus annuus* (Watkinson et al., 1983), *Impatiens pallida* (Weiner and Thomas, 1992), *Pennisetum americanum* (Schwinning, 1996), *Kochia scoparia* (Weiner and Fishman, 1994), *Brassica napus* L. (Damgaard, 1999), and *Chenopodium album* (Damgaard et al., 2002). In mono-specific, even-aged and spatially heterogeneous stands of black spruce (*Picea mariana*), both resource depletion and resource pre-emption processes were identified (Newton and Jolliffe, 1998). Our results suggest that the strength of pre-emption processes increase more sharply with density than does the strength of depletion processes. This leads to an increasing overall asymmetry of competition and therefore growth at higher densities.

The degree of growth asymmetry observed at different thinning intensities in this study is an expression of the average growth pattern during the time the plots were measured as trees grew (i.e. a probably varies across time). As a stand ages, the effect of competitive processes may vary because of changes in stand characteristics, size, limiting resources and age-dependent physiological changes within the trees. Competitive processes were similar among 25-50 year-old stands of cedar-hemlock forests, but these contrasted sharply with 11 year-old stands (Simard and Sachs, 2004). There is also evidence that the expression of the resulting competitive processes may vary as a result of variation in resource availability (Weiner, 1985; Knox et al., 1989; Cescatti and Piutti, 1998). Medium and large trees of Sitka spruce (*Picea sitchensis* Bong. Carr.) in an even-aged stand was found to respond more vigorously to increasing water availability hereby expressing increasing asymmetry of competition (Wichmann, 2001, 2002). Similarly, differentiation in unthinned stands of Sitka spruce was more pronounced in fertile stands, indicating that ample below-ground resources lead to a more pronounced asymmetric growth (Skovsgaard, 1997). Thus, increased avail-

ability of belowground resources results in an increase in competition for light, and therefore increased asymmetric growth. Since a varies with the relative importance of above- versus belowground competition, it may be useful in interpreting the growth dynamics of forest stands and the relative roles of competition for light and soil resources.

The degree of asymmetric growth has been assessed by measuring the size-inequality of the plant population (Weiner and Solbrig, 1984; Weiner and Thomas, 1986; Knox et al., 1989; Weiner, 1990). One approach to describe inequality of plant size is with the Lorenz-curve and the Gini-coefficient. The Lorenz-curve depicts the cumulative plant size when individuals are ranked according to their size (Lorenz, 1905; Damgaard and Weiner, 2000). Based on the Lorenz-curve of a theoretical population in which all individuals are equal to the mean (line of equality), the Gini-coefficient expresses the ratio of the area between the line of equality and the Lorenz-curve to the area under the line of equality. The depiction of Gini-coefficients (based on squared diameter) across stand ages of the individual plots (Figure V.4) show a clear distinction between the thinning regime by Jagd on one side (plots B1-C2) and unthinned controls (E1-E2) and the thinning regime by Bavngaard (plots A1, A2, D1 and D2) on the other. Although we found the asymmetric growth to be largest in the dense, unthinned plots, size-inequality is apparently largest in the plots subjected to the Bavngaard thinning regime. This is not surprising, since the Bavngaard regime aims at actively maintaining a vigorous understorey and hence a large diversity of sizes compared to the Jagd regime and the unthinned controls. The size inequality of these stands is not primarily a result of the competitive processes but rather a direct result of the thinning practices. This emphasizes the need for dynamic measures of size-asymmetric growth in managed forest stands.

Recent developments in computational statistics afford us the opportunity to break down the distinction between theoretical and statistical modelling in ecology. We can now build and fit biologically based (and biologically-motivated) models, i.e. models in which the parameters have clear biological interpretations, that until a few years ago one would not even think of fitting to real data. In this study, competition among individuals was modelled by simultaneously coupling differential equations for the individual trees. Thus, each plant's growth rate is affected not only by its own size and growth parameters but also by the cumulative size of all the other individuals in the population. The relationship between individual plant size and growth rate across the population contains important information about the size symmetry of competition among individuals. Explicit modelling of this relationship represents another level of information which offers the possibility of bridging the gap between predictive and descriptive models of forest growth.

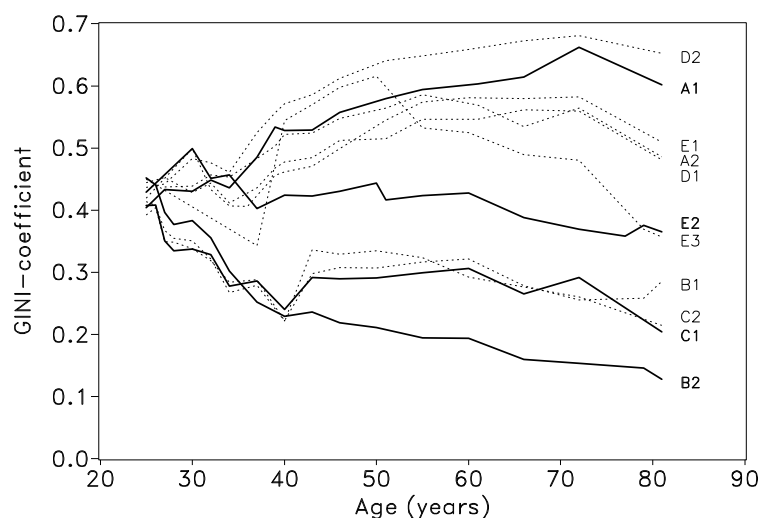


Figure V.4: Gini-coefficients as a function of stand age for the individual plots. The four plots used in the analysis, A1 (Bavngaard), B2 (Jagd), C1 (Jagd) and E2 (unthinned control), are represented by the full black lines whereas the other plots are presented by dotted lines.

References

- Carlin, B. P. and Louis, T. A. (1996). *Bayes and empirical Bayes methods for data analysis*. Chapman & Hall, London. 440 p.
- Casper, B. B. and Jackson, R. B. (1997). Plant competition underground. *Annu. Rev. Ecol. Syst.*, 28:545–570.
- Cescatti, A. and Piutti, E. (1998). Silvicultural alternatives, competition regime and sensitivity to climate in a European beech forest. *For. Ecol Man.*, 102:213–223.
- Damgaard, C. (1999). A test of asymmetric competition in plant monocultures using the maximum likelihood function of a simple growth model. *Ecological Modelling*, 116:285–292.
- Damgaard, C. and Weiner, J. (2000). Describing inequality in plant size or fecundity. *Ecology*, 81:1139–1142.
- Damgaard, C., Weiner, J., and Nagashima, H. (2002). Modelling individual growth and competition in plant populations: growth curves of *cheopodium album* at two densities. *Journal of Ecology*, 90:666–671.
- Dent, J. B. and Blackie, M. J. (1979). *Systems Simulation in Agriculture*, pages 94–117. Applied Science Publishers ltd., London. 180 p.

-
- Durbin, J. and Watson, G. S. (1950). Testing for serial correlation in least squares regression i. *Biometrika*, 37:409–428.
- García, O. (1983). A stochastic differential equation model for height growth of forest stands. *Biometrics*, 39:1059–1072.
- Gertner, G. Z. (1985). Efficient nonlinear model estimation: Its relationship to measurement interval. *For. Sci.*, 31:821–826.
- Holmsgaard, E. (1985). Self-pruning, formation of epicormic shoots etc. during 25 years in a non-thinned and two thinned plots of a thinning experiment in beech. *Det Forstlige Forsøgsvæsen*, 38:1–51.
- Johannsen, V. K. (2002). Selection of diameter-height curves for even-aged oak stands in Denmark. Dynamic growth models for Danish forest tree species, Working paper 16, Danish Forest and Landscape Research Institute, Hørsholm, Denmark. 70 p.
- Knox, R. G., Peet, R. K., and Christensen, N. (1989). Population dynamics in loblolly pine stands: changes in skewness and size inequality. *Ecology*, 70:1153–1166.
- Lorenz, M. O. (1905). Methods for measuring the concentration of wealth. *American Statistics Association*, 9:209–219.
- Madsen, S. F. (1987). Volume equations for some important Danish forest tree species. *Det Forstlige Forsøgsvæsen*, 40:47–242.
- McDill, M. E. and Amateis, R. E. (1993). Fitting discrete-time dynamic models having any time interval. *For. Sci.*, 39:499–519.
- Näslund, M. (1936). Skogsforsöksastaltens gallringsforsök i tallskog. *Meddelanden från Statens Skogsforsöksanstalt*, 29:1–169.
- Newton, P. F. and Jolliffe, P. (1998). Assessing processes of intraspecific competition within spatially heterogeneous black spruce stands. *Can. J. For. Res.*, 28:259–275.
- Reed, D. D. and Burkhart, H. E. (1985). Spatial autocorrelation of individual tree characteristics in loblolly pine stands. *For. Sci.*, 31:575–587.
- Richards, F. J. (1959). A flexible growth equation for empirical use. *Journal of Experimental Botany*, 10:290–300.
- Schwinning, S. (1996). Decomposition analysis of competitive symmetry and size structure dynamics. *Annals of Botany*, 77:422–432.
- Schwinning, S. and Fox, G. A. (1995). Competitive symmetry and its consequences for plant population dynamics. *Oikos*, 72:422–432.

- Schwinning, S. and Weiner, J. (1998). Mechanisms determining the degree of size-asymmetry in competition among plants. *Oecologia*, 113:447–455.
- Seber, G. A. F. and Wild, C. J. (1989). *Nonlinear Regression*. Wiley series in probability and mathematical statistics. Wiley, New York. 768 p.
- Simard, S. W. and Sachs, D. L. (2004). Assessment of interspecific competition using relative height and distance indices in an age sequence of seral interior cedar-hemlock forests in British Columbia. *Can. J. For. Res.*, 34:1228–1240.
- Skovsgaard, J. P. (1997). *Tyndingsfri drift af sitkagran*. Forskningsserien no. 19. Forskningscentret for Skov & Landskab, Hørsholm, Denmark. 525 p.
- Vancley, J. K. (1994). *Modelling Forest Growth and Yield*. CAB International, Wallingford, United Kingdom. 312 p.
- Watkinson, A. R., Lonsdale, W. M., and Firbank, L. G. (1983). A neighbourhood approach to self-thinning. *Oecologia*, 56:381–384.
- Weiner, J. (1985). Size hierarchies in experimental populations of annual plants. *Ecology*, 66:743–752.
- Weiner, J. (1990). Asymmetric competition in plant populations. *Trends in Ecology and Evolution*, 5:360–364.
- Weiner, J. and Fishman, L. (1994). Competition and allometry in *Kochia scoparia*. *Annals of Botany*, 73:263–271.
- Weiner, J., Kinsman, S., and Williams, S. (1998). Modelling the growth of individuals in plant populations: local density variation in a strand population of *Xanthium strumarium* (Asteraceae). *American Journal of Botany*, 85:1638–1645.
- Weiner, J. and Solbrig, O. (1984). The meaning and measurement of size hierarchies in plant populations. *Oecologia*, 61:334–336.
- Weiner, J. and Thomas, S. C. (1986). Size variability and competition in plant monocultures. *Oikos*, 47:211–222.
- Weiner, J. and Thomas, S. C. (1992). Competition and allometry in three species of annual plants. *Ecology*, 73:648–656.
- Weiner, J., Wright, D. B., and Castro, C. J. (1997). Symmetry of below-ground competition between *Kochia scoparia* individuals. *Oikos*, 79:85–91.

- Wichmann, L. (2001). Annual variations in competition symmetry in even-aged Sitka spruce. *Annals of Botany*, 88:145–154.
- Wichmann, L. (2002). *Modelling the effects of competition between individual trees in forest stands*. PhD thesis, Royal Veterinary and Agricultural University. Copenhagen, Denmark. 112 p.
- Wolfram, S. (2003). *The Mathematica Book*. Cambridge University Press, Cambridge, United Kingdom, 4 edition. 1470 p.
- Wyszomirski, T., Wyszomirska, I., and Jarzyna, I. (1999). Simple mechanisms of size distribution dynamics in crowded and uncrowded virtual monocultures. *Ecological modelling*, 115:253–273.

Paper VI

**A spatially explicit
individual-tree model**

A spatially explicit individual-tree model

Thomas Nord-Larsen ^{*1}

^{*}Royal Veterinary and Agricultural University, Forest & Landscape,
Hørsholm Kongevej 11, DK-2970 Hørsholm, Denmark

Abstract

Spatial individual-tree models are important tools for understanding processes of forest growth. However, spatial models often bring little if any improvement compared to a (good) non-spatial model. Based on 16 permanent thinning experiments a series of spatial and non-spatial indices of competition were evaluated for predicting diameter growth of European beech in Denmark. Results showed that models including some measure of competition performed better than models that did not include such measures. Judged from the results, the use of spatially explicit indices of competition did not improve the model's ability to predict individual-tree growth. This result is discussed in relation to the inclusion of random spatio-temporal effects in spatial individual-tree growth models.

Keywords: *Fagus sylvatica*, Bayes, mixed effects models

Introduction

The shortcomings of stand-level growth models for predicting forest growth has become increasingly clear as the political awareness of the need for sustainable forest management has created a demand for uneven-aged management of mixed-species forests. The aggregation made by using for instance a yield table for planning or research purposes may be valid for monospecific, even-aged management because even-aged monocultures are relatively homogeneous. Similarly, a mean-field (spatially implicit) individual-tree growth model may work relatively well in evenly spaced monocultures, where the competition among individual trees is homogeneous across the stand. However, as stands become increasingly diverse, the spatial and temporal heterogeneity increases and at some point existing growth models are no longer applicable because they do not include the effects of the spatial and temporal distribution of individual trees.

The effect of the spatial arrangement of the individual trees on tree growth was first recognized by the Danish forester C.D.F. Reventlow in 1816 (c.f. Holten-Andersen, 1989). It is however just in recent decades that it has become possible to explicitly model the complex competitive interactions

¹Corresponding author. E-mail: tnl@kvl.dk, Phone (+45) 35281758, Fax (+45) 35281517

among individual trees (Opie, 1962; Tomé and Burkhart, 1989; Biging and Dobbertin, 1992; Pukkala, 1989; Pretzsch, 1997). Most of these studies have found that although spatial measures of competition provided useful insight to the effects of competition, they only provided little improvement in predicting individual-tree growth compared to a mean field model.

To assess the importance of the spatial arrangement of individual trees when modelling growth, a preliminary study is conducted using various spatially explicit individual-tree growth models and comparing their predictions with those of a mean field model. Thus, the underlying hypothesis is that the spatial arrangement of individual trees influences individual-tree growth and that the effect can be quantified in a mathematical model. Further, it is hypothesized that the spatial competition indices more appropriately express competition and hence results in better estimates of individual-tree growth.

Materials

The data for spatially explicit modelling growth of European beech in Denmark originate from 16 permanent thinning experiments including 20 individual plots. Plot sizes vary between 0.10 and 2.2 ha with an average of 0.55 ha. The experiments are all located in the eastern parts of Denmark where the growth conditions are more suitable for growing beech than the sandy soils in western Denmark. The data were collected during the period from 1903 to 2004 and includes a total of 305 measurement occasions.

The individual trees are positioned on every plot (Figure VI.1). Measurements of diameter are obtained by averaging two perpendicular calliper readings taken at breast height (1.3 m) for each tree. Observations also include records on whether the tree is alive or dead at the time of measurement. Individual height of live trees was measured using a hypsometer and felled trees were measured on the ground using a tape measure. The data include 25,617 individual diameter measurements and 5,886 height measurements.

Methods

Diameter increment of individual trees (Δd_i), may be described as a function of tree size (d_i) and some measure of the competition experienced by the individual tree, modelled either as a spatially explicit competition index (CI_i) or as a measure of the mean competition within the stand. A large variety of mathematical models have been used to describe individual-tree increment. Despite this seeming variety, many of the models may be reduced to entail only two competing factors: the biological potential for unlimited multiplicative growth and a reduction due to aging and environmental constraints (Zeide, 1993). Hence individual-tree growth may be described as

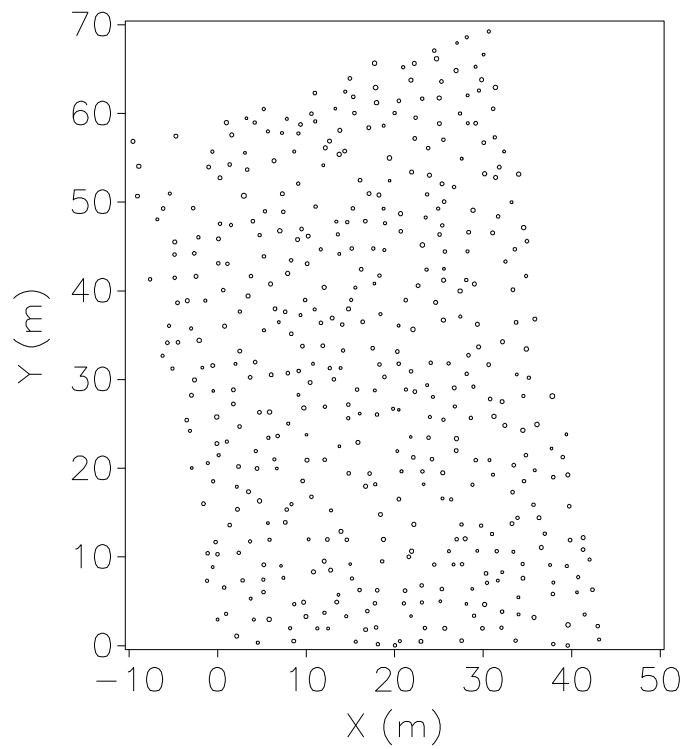


Figure VI.1: An example of a stem-map from experiment BL in Grib Skov, Northern Zealand. The stem-map is from 1904, when the stand was first mapped, but the stand was measured regularly until 1997.

an initial multiplicative expansion that is increasingly dampened as the tree grows larger. This growth pattern was modelled by a function with a multiplicative term and exponential dampening:

$$\Delta d_i = \alpha d_i^\beta e^{-\gamma d_i} \quad (\text{VI.1})$$

The resulting cumulative growth curve has a sigmoid form but no asymptote.

Competition indices The effect of competition on individual-tree growth may be modelled in a variety of ways. In so-called mean field models competition experienced by the individual tree is described by stand-level measures of density regardless of the distance between individual trees. Examples of such measures of competition are basal area, G ($m^2 ha^{-1}$) and basal area of trees larger than the subject tree, G_L ($m^2 ha^{-1}$).

In heterogeneous forests such measures of competition would break down as the stand-level density does not describe the local level of competition. Intuitively, spatially explicit measures of competition would perform better in this case. A large number of different spatially explicit competition indices have been developed for application in tree growth models. Among the different indices those developed by Hegyi (1974) (H), Martin and Ek (1984) (ME), Bella (1971) (B), and Schneider et al. (2005) (L) were chosen for this study:

$$CI_H = \sum_{i \neq j} e_i \frac{d_j}{d_i(Dist_{ij} + 1)} \quad (\text{VI.2})$$

$$CI_{ME} = \sum_{i \neq j} e_i \frac{d_j}{d_i} \exp\left(\frac{-16 Dist_{ij}}{d_i + d_j}\right) \quad (\text{VI.3})$$

$$CI_B = \sum_{i \neq j} e_i \frac{O_{ij} d_j}{Z_i d_i} \quad (\text{VI.4})$$

$$CI_L = \sum_{i \neq j} e_i \frac{O_{ij}}{2} (1 + \tanh(\rho(r_j - r_i))) \quad (\text{VI.5})$$

where $Dist_{ij}$ is the distance between the competitor and the subject tree, Z_i is the influence zone (crown surface area) of the subject tree, O_{ij} is the overlap of the circular influence zones of i and j , and e is a linear expansion factor for the control of plot edge bias. ρ is an indicator of competition asymmetry, which was set at 0, 1, and 2, providing three different forms of CI_L (CI_{L0} , CI_{L1} , and CI_{L2}). Crown surface area was estimated as a function of diameter (d) and height (h) (Pretzsch et al., 2002):

$$Z_i = \exp(0.8556 + 0.4299 \ln(d_i) + -0.0035h + -0.3238 \ln(h/d)) \quad (\text{VI.6})$$

Estimation The data has a simple three-layer hierarchical structure with individual measurements on individual trees nested within different forest stands. The model was estimated using a hierarchical mixed-effects model and the estimation problem may be formulated as:

$$\Delta d_{ijk} = \beta_1 d_i \beta_2 e^{\beta_3 d_i} e^{\beta_4 C I_i} e^{u_{plot(i)} + v_{tree(i)} + \varepsilon_i} \quad (\text{VI.7})$$

where $u_{plot} \sim N(0, \sigma_p^2)$ and $v_{tree} \sim N(0, \sigma_t^2)$ are the random effects of plots and individual trees, $\varepsilon_i \sim N(0, \sigma^2)$ is the "white noise", $\beta_1 - \beta_4$ are parameters to be estimated and $C I_i$ is some measure of competition for the individual tree.

For the estimation procedure, the structure of repeated measurements on the individual tree was ignored as the increments in different periods were assumed to be uncorrelated. Bayesian posterior distributions were first calculated for the nonlinear mixed effects model, assuming an uninformative, uniform prior distribution with a burn in of 50.000 iterations using winBUGS. However, despite the long burn-in the generated values of the parameters exhibited poor mixing properties suggesting large correlation between individual parameters. To reduce this problem the model was reparameterized as:

$$\Delta d_{ijk} = \beta_0 \left(\frac{d_i}{\tilde{D}} \right)^{\beta_2} e^{\beta_3 d_i} e^{\beta_4 C I_i} e^{u_{plot(i)} + v_{tree(i)} + \varepsilon_i}, \quad (\text{VI.8})$$

$$\beta_0 = \left(\beta_1 \tilde{D}^{\beta_2} \right), \quad (\text{VI.9})$$

$$\tilde{D} = \left(\prod_{i=1}^n d_i \right)^{\frac{1}{n}} \quad (\text{VI.10})$$

Although the properties of the model were improved considerably, convergence was slow due to the large number of random parameters. Consequently, the problem was analyzed in MLwin after having linearized equation (VI.7):

$$\log(\Delta d_i) = \beta_1 + \beta_2 \log(d_i) + \beta_3 d_i + \beta_4 C I_i + u_j + v_k + \varepsilon_i \quad (\text{VI.11})$$

As some of the observed increments are negative due to measurement error, the log-transformation creates missing values for a number of observations. In those cases, increment was set to a small value (0.01 mm). The linearized model was estimated using a burn-in period of 10,000 iterations and a monitoring period of 50.000 iterations. The parameters of equation (VI.11) were estimated for a NULL model, where no competition effect was included in the model, for a mean-field model (where $\beta_4 C I_i = \beta_4 G + \beta_5 G_{L,i}$), and for the models including various spatial competition indices ((VI.2) - (VI.5)).

The performance of the competition indices was evaluated from the DIC statistic of the different models:

$$DIC = -2\log L(data \mid \bar{\theta}) + 2p_D \quad (\text{VI.12})$$

where $\log L(data \mid \bar{\theta})$ is the deviance at the posterior mean ($\bar{\theta}$) and p_D is an estimate of the effective number of parameters.

Results

Compared to the non-linear estimation in winBUGS, the different linear models estimated in MLwin had excellent mixing properties. The burn-in period of 10,000 iterations and monitoring period of 50,000 iterations exceeded the required number of iterations (Raftery-Lewis) by a factor of 8-10. Kernel-densities of the individual parameters were almost normally distributed. Residuals were not normally distributed, which was expected because zero and negative growth were given a fixed, low value. However, the non-normality of residuals was not judged to influence parameter-estimates given the size of the data.

The parameters estimated for each of the different competition indices confirmed the prior notion of initial multiplicative growth followed by exponential dampening (Table VI.1). Further, the signs of the parameter estimates confirmed that competition had a negative effect upon individual-tree growth. The DIC statistic showed that models including some measure of competition performed better than the model without such measure. However, judged from the DIC values, the use of spatially explicit indices of competition does not result in any improvements in the model's ability to predict individual-tree growth.

Discussion

The analyses of various spatial and non-spatial competition indices indicate that spatially explicit indices of competition do not improve predictions of tree growth compared to the non-spatial alternative. The poor performance of the spatial models compared to the non-spatial model may in part be due to the homogeneity of the stands included in this study and hence that the spatial effects are difficult to observe. Another reason may be that the competition indices chosen for this study are very simple and may not be adequate for the modelling purpose. The simple indices used in this study are generally viewed as inferior to other, more complex indices such as Area Potentially Available (APA) (Tomé and Burkhart, 1989).

The failure of spatially explicit individual-tree growth models to produce consistently better results than non-spatial models is also observed in most other studies comparing spatial and non-spatial models (e.g. Biging

Table VI.1: Statistics of the Bayesian estimation procedure after a burn-in of 10,000 iterations and a monitoring period of 50,000 iterations for different competition indices (Equation (VI.11)). Variance of the parameter estimates are given in parentheses.

Model	β_1	β_2	β_3	β_4	β_5	σ^2	$\sigma_{v(tree)}^2$	$\sigma_{u(plot)}^2$	DIC
<i>Null</i>	-12.618 (0.418)	2.772 (0.079)	-0.007 (0.000)	.	.	1.038 (0.012)	0.414 (0.019)	0.591 (0.248)	62869.13
<i>Meanfield</i>	-10.124 (0.384)	2.592 (0.076)	-0.007 (0.000)	-0.016 (0.002)	-0.055 (0.002)	0.982 (0.011)	0.372 (0.016)	0.295 (0.128)	61656.23
<i>CI_H</i>	-10.837 (0.442)	2.483 (0.084)	-0.006 (0.000)	-0.236 (0.024)	.	1.031 (0.011)	0.421 (0.019)	0.471 (0.196)	62745.01
<i>CI_{ME}</i>	-11.583 (0.397)	2.701 (0.077)	-0.007 (0.000)	-0.368 (0.020)	.	1.015 (0.011)	0.428 (0.019)	0.454 (0.190)	62437.49
<i>CI_B</i>	-14.734 (0.384)	3.291 (0.079)	-0.007 (0.000)	-0.143 (0.005)	.	1.015 (0.011)	0.369 (0.016)	0.553 (0.230)	62327.37
<i>CI_{L0}</i>	-14.646 (0.398)	3.255 (0.078)	-0.007 (0.000)	-0.295 (0.014)	.	1.019 (0.011)	0.401 (0.017)	0.602 (0.250)	62470.45
<i>CI_{L1}</i>	-14.619 (0.392)	3.255 (0.077)	-0.008 (0.000)	-0.165 (0.007)	.	1.020 (0.011)	0.381 (0.017)	0.563 (0.234)	62441.52
<i>CI_{L2}</i>	-14.603 (0.392)	3.251 (0.077)	-0.008 (0.000)	-0.163 (0.007)	.	1.020 (0.011)	0.381 (0.017)	0.563 (0.234)	62444.47

and Dobbertin, 1992). One explanation may be that the effect of temporal variation on competition among trees are not well understood and thus not adequately captured by the models. Several studies have indicated that availability of nutrients and water essentially influences competition asymmetry and hence the competition experienced by the individual tree (Weiner, 1985; Knox et al., 1989; Skovsgaard, 1997; Cescatti and Piutti, 1998; Wichmann, 2002). These findings may indicate that a relatively simple spatial competition index that does not include the effect of climatic variation does not adequately express the competition experienced by the individual tree. Hence, such index may not predict individual-tree increment any better than a simple non-spatial measure of competition.

Although methodologies are currently developing to better describe the underlying mechanisms of tree growth, the vast majority of growth models remains overly simplistic and thus entails large amounts of unexplained variation. Although much of the variation in growth may not be captured by a deterministic model, the variation may be incorporated in the stochastic structure of the individual-tree growth model (Stage and Wykoff, 1993). Such mixed effect models include both the variation that may be attributed to known effects (fixed effects) and variation that can only be included by a stochastic representation of the underlying, unknown effects (random effects).

In spatial individual-tree growth models the stochastic structure of data may have several components on different hierarchical levels (e.g. individual trees, plots, or experiments; Fox et al., 2001). The error structure is said to be "nested" as multiple measures are taken from individual sampling units and combined across those units. For instance, several measurements may be taken on individual trees within several plots located within a number of different forests. If the differences among individual trees, plots, or forests are not fully explained by the model (e.g. unexplained genetic differences or differences in growth patterns), model errors are correlated and OLS estimates lead to reduced estimation efficiency and biased estimates of standard errors of the parameters. The problem may be overcome by mixed models where fixed effects and random effects on the tree, plot, and stand-level are estimated simultaneously (Gregoire, 1987) as in the present study.

An error component not included in this study although present in most forest growth data eventuates when more measurements are taken on the same individual (or stand for stand-level models) over time. Due to temporal variations (such as rainfall, temperature, long-term fluctuations in climate etc.) observations on the same tree are correlated and the similarity of observations increases with temporal proximity of observations. Failure to include the variables explaining the temporal variation leads to error correlations. Characterization of the temporal dependence of observations have been demonstrated by a number of authors (García, 1983; Gregoire, 1987; Miina, 1993; Stage and Wykoff, 1993) and was included in both the

stand-level and individual-tree growth models presented in Appendix II and IV.

In forest stands variation in soil properties and microclimate across the stand or differences in competition causes the growth of neighbouring trees to be correlated. To the extent that these variations are not modelled adequately the spatial variation gives rise to error correlations. Contrary to the stochastic nested and temporal error structures, stochastic spatial error structures have largely been omitted by modellers of forest growth. However, when spatial influences are not fully captured in the model, model inference will be biased. Strong micro-site variations may mask the influences of competition (micro-site variation will produce positive spatial correlations whereas competition produces negative correlations), leading to the counter-intuitive conclusion that the spatial arrangement of trees has no effect on tree growth. This may be the cause of the surprising conclusion of this study; that inclusion of spatial effects provides no improvement of individual-tree growth predictions compared to the non-spatial model.

Forest growth data are often both cross-sectional and longitudinal and are thus likely to have both hierarchical, temporal, and spatial correlation structures. So far all the different error components have never been included in a stochastic individual-tree growth model because computational demands increase rapidly with the complexity of the error structure of a model. However, new hierarchical Bayes methodologies and the development of sampling-based algorithms offer flexibility in the analysis of complex ecological problems such as tree growth. It thus remains a challenge and an area of active research to develop models of forest growth that simultaneously include the hierarchical and spatio-temporal structures.

Literature cited

- Bella, I. E. (1971). A new competition model for individual trees. *For. Sci.*, 17:364–372.
- Biging, G. S. and Dobbertin, M. (1992). A comparison of distance dependent competition measures for height and basal area growth of individual trees. *For. Sci.*, 38:695–720.
- Cescatti, A. and Piutti, E. (1998). Silvicultural alternatives, competition regime and sensitivity to climate in a European beech forest. *For. Ecol. Man.*, 102:213–223.
- Fox, J. C., Ades, P. K., and Bi, H. (2001). Stochastic structure and individual-tree growth models. *For. Ecol. Man.*, 154:261–276.
- García, O. (1983). A stochastic differential equation model for height growth of forest stands. *Biometrics*, 39:1059–1072.

- Gregoire, T. G. (1987). Generalized error structure for forestry yield models. *For. Sci.*, 33:423–444.
- Hegyi, F. (1974). A simulation model for managing Jack pine stands. In Fries, J., editor, *Growth models for tree and stand simulations*, pages 74–90. Royal College of Forestry, Stockholm, Sweden.
- Holten-Andersen, P. (1989). Danish yield tables in the past century. *Det Forstlige Forsøgsvæsen i Danmark*, 42:71–145.
- Knox, R. G., Peet, R. K., and Christensen, N. (1989). Population dynamics in loblolly pine stands: changes in skewness and size inequality. *Ecology*, 70:1153–1166.
- Martin, G. L. and Ek, A. R. (1984). A comparison of competition measures and growth models for predicting plantation red pine diameter and height growth. *For. Sci.*, 30:731–743.
- Miina, J. (1993). Residual variation in diameter growth in a stand of Scots pine and Norway spruce. *For. Ecol. Man.*, 58:111–128.
- Opie, J. E. (1962). Predictability of individual tree growth using various definitions of competing basal area. *For. Sci.*, 14:314–323.
- Pretzsch, H. (1997). Analysis and modelling of spatial stand structures. Methodological considerations based on mixed beech-larch stands in Lower Saxony. *For. Ecol. Man.*, 97:237–253.
- Pretzsch, H., Biber, P., and Dürský, J. (2002). The single tree-based stand simulator SILVA: construction, application and evaluation. *For. Ecol. Man.*, 162:3–21.
- Pukkala, T. (1989). Predicting diameter growth in even-aged Scots pine stands with a spatial and non-spatial model. *Silvia Fennica*, 23:101–106.
- Reventlow, C. D. F. (1816). Formeentlige Resultater af en deel Fortsatte Undersøgelser angaaende indflydelsen af Træernes gjensidige Afstand på deres mere eller mindre Fordelagtige Vegetation. *Det Kongelige Danske Videnskabernes Selskabs skrifter for aar 1809, 1810, 1811 og 1812*. 3. Række, 6. Bind, II. Hæfte.
- Schneider, M. K., Law, R., and Illian, J. B. (2005). Quantification of neighbourhood-dependent plant growth by Bayesian hierarchical modelling. *Journal of Ecology*, In press.
- Skovsgaard, J. P. (1997). *Tyndingsfri drift af sitkagran*. Forskningsserien no. 19. Forskningscentret for Skov & Landskab, Hørsholm, Denmark. 525 p.

- Stage, A. A. and Wykoff, W. R. (1993). Calibrating a model of stochastic effects on diameter increment for individual-tree simulations of stand dynamics. *For. Sci.*, 39:692–705.
- Tomé, M. and Burkhart, H. E. (1989). Distance-dependent competition measures for predicting growth of individual trees. *For. Sci.*, 35:816–831.
- Weiner, J. (1985). Size hierarchies in experimental populations of annual plants. *Ecology*, 66:743–752.
- Wichmann, L. (2002). *Modelling the effects of competition between individual trees in forest stands*. PhD thesis, Royal Veterinary and Agricultural University. Copenhagen, Denmark. 112 p.
- Zeide, B. (1993). Analysis of growth equations. *For. Sci.*, 39:594–616.

Appendices

Appendix A

Examples of yield tables for beech

Table A.1: Yield table for a B-grade thinning regime based on the stand-level model. Calculations were carried out by Anders Lomholt (B.Sc.) as part of his master thesis.

Age	Remaining crop						Thinning						Increment	
	H_{100}	H_g	m	N	G	D_g	V	RS	N	G	D_g	V	Q	I_v
Years	m	m	m	ha^{-1}	$m^2 ha^{-1}$	cm	$m^3 ha^{-1}$	ha^{-1}	ha^{-1}	$m^2 ha^{-1}$	cm	$m^3 ha^{-1}$	$m^3 ha^{-1} year^{-1}$	
25	9.1	7.7	5000	16.00	6.4	51.7	0.18	0	0.00	7.2	0.0	1.0	2.1	
30	11.8	10.6	4549	22.40	7.9	110.8	0.14	451	1.76	7.1	8.4	0.9	13.5	
35	14.7	13.5	2787	20.60	9.7	135.1	0.14	1763	9.42	8.2	60.4	0.9	16.9	
40	17.2	16.2	1940	20.40	11.6	160.8	0.14	847	6.66	10.0	52.1	0.9	15.6	
45	19.3	18.4	1513	21.40	13.4	191.9	0.14	427	4.64	11.8	41.5	0.9	14.5	
50	21.1	20.3	1240	22.60	15.2	223.7	0.14	273	3.88	13.4	38.2	0.9	14.0	
55	22.6	21.9	1058	24.00	17.0	257.2	0.14	182	3.23	15.1	34.4	0.9	13.6	
60	24.0	23.4	939	25.70	18.7	294.3	0.14	119	2.57	16.6	29.3	0.9	13.3	
65	25.3	24.6	834	27.00	20.3	327.1	0.14	105	2.68	18.1	32.2	0.9	13.0	
70	26.4	25.8	770	28.80	21.8	366.5	0.14	64	1.92	19.5	24.3	0.9	12.7	
75	27.4	26.9	702	30.00	23.3	398.7	0.14	68	2.31	20.8	30.4	0.9	12.5	
80	28.3	27.8	655	31.50	24.7	435.2	0.14	47	1.81	22.1	24.7	0.9	12.2	
85	29.1	28.7	593	32.00	26.2	458.0	0.14	62	2.64	23.4	37.3	0.9	12.0	
90	29.9	29.5	531	32.00	27.7	472.9	0.15	62	2.98	24.7	43.4	0.9	11.7	
95	30.6	30.3	478	32.00	29.2	487.1	0.15	53	2.83	26.0	42.5	0.9	11.3	
100	31.3	31.0	432	32.00	30.7	500.4	0.16	46	2.71	27.4	41.7	0.9	11.0	
105	31.9	31.6	392	32.00	32.3	513.2	0.16	40	2.59	28.7	41.0	0.9	10.7	
110	32.4	32.2	357	32.00	33.8	525.4	0.16	35	2.49	30.1	40.3	0.9	10.5	
115	33.0	32.7	326	32.00	35.4	537.2	0.17	31	2.40	31.5	39.6	0.9	10.3	
120	33.5	33.3	299	32.00	36.9	548.6	0.17	27	2.32	32.9	39.0	0.9	10.1	
125	33.9	33.7	275	32.00	38.5	559.7	0.18	24	2.24	34.4	38.5	0.9	9.9	
130	34.4	34.2	253	32.00	40.1	570.5	0.18	22	2.17	35.8	38.0	0.9	9.8	
135	34.8	34.6	234	32.00	41.8	581.1	0.19	19	2.11	37.3	37.6	0.9	9.6	
140	35.2	35.0	234	34.05	43.1	628.6	0.19	0	0.00	0.0	0.0	0.0	9.5	

Table A.2: Yield table for a C-grade thinning regime based on the stand-level model. Calculations were carried out by Anders Lomholt (B.Sc.) as part of his master thesis.

Age	Remaining crop						Thinning						Increment
	H_{100}	H_g	N	G	D_g	V	RS	N	G	D_g	V	Q	I_v
Years	m	m	ha^{-1}	m^2ha^{-1}	cm	m^3ha^{-1}		ha^{-1}	m^2ha^{-1}	cm	m^3ha^{-1}		$m^3ha^{-1}year^{-1}$
25	9.1	7.7	5000	16.00	6.4	51.7	0.18	0	0.00	7.2	0.0	1.0	2.1
30	11.8	10.6	2761	15.40	8.4	77.5	0.18	2239	8.76	7.1	41.7	0.9	13.5
35	14.5	13.3	1740	15.70	10.7	102.1	0.18	1021	6.71	9.1	43.1	0.9	13.5
40	16.8	15.8	1244	16.80	13.1	129.9	0.18	496	5.04	11.4	38.8	0.9	13.3
45	18.9	17.9	962	18.20	15.5	160.2	0.18	283	4.10	13.6	35.9	0.9	13.2
50	20.6	19.8	787	19.80	17.9	192.9	0.18	175	3.41	15.8	33.0	0.9	13.2
55	22.2	21.4	671	21.50	20.2	227.7	0.18	116	2.92	17.9	30.7	0.9	13.1
60	23.6	22.9	591	23.30	22.4	264.8	0.18	80	2.50	19.9	28.1	0.9	13.0
65	24.8	24.2	529	25.00	24.5	301.8	0.18	62	2.32	21.8	27.7	0.9	12.9
70	26.0	25.4	477	26.50	26.6	337.3	0.18	52	2.28	23.7	28.6	0.9	12.8
75	27.0	26.5	439	28.10	28.6	374.8	0.18	38	1.96	25.5	25.8	0.9	12.7
80	27.9	27.4	396	29.00	30.5	403.5	0.18	42	2.47	27.2	33.8	0.9	12.5
85	28.8	28.3	348	29.00	32.6	419.4	0.19	48	3.19	28.9	45.4	0.9	12.2
90	29.5	29.1	307	29.00	34.7	434.4	0.20	41	3.02	30.8	44.5	0.9	11.9
95	30.3	29.9	273	29.00	36.8	448.6	0.20	34	2.87	32.7	43.6	0.9	11.6
100	30.9	30.6	244	29.00	38.9	462.3	0.21	29	2.74	34.6	42.9	0.9	11.3
105	31.5	31.2	219	29.00	41.1	475.4	0.22	25	2.63	36.6	42.2	0.9	11.1
110	32.1	31.8	197	29.00	43.3	488.2	0.22	22	2.53	38.5	41.6	0.9	10.9
115	32.6	32.4	178	29.00	45.5	500.6	0.23	19	2.44	40.5	41.1	0.9	10.7
120	33.1	32.9	162	29.00	47.8	512.8	0.24	17	2.35	42.6	40.6	0.9	10.6
125	33.6	33.4	147	29.00	50.1	524.8	0.25	15	2.27	44.6	40.1	0.9	10.4
130	34.0	33.8	135	29.00	52.4	536.6	0.25	13	2.20	46.7	39.7	0.9	10.3
135	34.4	34.3	123	29.00	54.8	548.4	0.26	11	2.14	48.9	39.4	0.9	10.2
140	34.8	34.7	123	31.08	56.7	599.1	0.26	0	0.00	0.0	0.0	0.0	10.1

Appendix B

The experiments

Table B.1: Overview of the individual experiments used in the analyses.

Experiment	District	Forest	Compartment	Source ¹	UTM zone	UTM E (m)	UTM N (m)	Objective	Plots ²	Established	Birth ³
1003	Bregentved	Nyskov	562	135	32	695279	6136415	Species	9	1964-65	1961-63
1004	Pederstrup-Christianssæde	Christianssæde	308	136	32	651929	6072566	Species	11	1964-65	1961-63
1005	Frijsenborg	St. Dyrehave	57	137	32	556085	6233934	Species	6	1964-65	1960-61
1007	Lindet	Lovrup	185	139	32	492634	6110713	Species	12	1964-65	1961-63
1008	Løvenholm	Marielund	7	140	32	594399	6258113	Species	12	1964-65	1961-63
1009	Palsgård	Hastrup	265	141	32	512950	6199394	Species	11	1964-65	1961-63
1010	Skjoldenæsholm	Højbjerg	292	142	32	678366	6158785	Species	11	1964-65	1961-63
1011	Frederiksborg	Stenholt	635	143	32	709370	6206263	Species	12	1964-65	1961-63
1012	Gråsten	Vang	301	144	32	540840	6085330	Species	8	1964-65	1961-63
1013	Hanherred	Skodsbøl	90:92	145	32	533226	6339015	Species	15	1964-65	1961-63
1014	Ulborg	Rødhus	9	146	32	464584	6238767	Species	12	1964-65	1961-63
1015	Nørlund	Katborg	140a	147	32	561968	6294317	Species	12	1964-65	1961-63
1195	Matrup	Nørskov	327	311	32	538554	6202014	Species	9	1973	1969-71
1196	Odsherred	Ring	193	312	32	669472	6192222	Species	10	1973	1969-71
1197	Petersgård	Stokkebjerg	27	313	32	701892	6101337	Species	10	1973	1969-71
1198	ValleStifts	Vienose	167	314	32	693775	6146186	Species	9	1973	1969-71
1199	Wedellsborg	Tågerød	69:70	315	32	553818	6139716	Species	8	1973	1969-71
1272	ValleStifts	Grevinde	52:53	377	32	694947	6151506	Mix species	7	1980	1976-78
1273	Gråsten	Skovhusv.	50	378	32	557667	6097218	Mix species	7	1981	1977-78
1283	Krenkerup	Nørreskov	15	12	32	673130	6070807	Species	11	1964	1945-48
1296	Fyns	Rykkerup	101	394	32	574766	6124764	Mix species	8	1983	1979-81
A	Falster	Lærkedal	735	Map	32	685696	6073524	Production	1	1871	1799
BL	Frederiksborg	Gribskov		Map	32	706425	6209591	Production	1	1893	1850
CA	Gurre	Danstrup						Production	1	1894	1796
CB	Kronborg	Hegn		Map	32	717522	6216233	Production	1	1894	1806
		Horserød									
		Hegn									

¹Numbers refer to the Establishment Report at *Forest & Landscape*, ²Total number of plots in the experiment of which all may not be beech, ³Seed year

Table B.1: Overview of the individual experiments used in the analyses.

Experiment	District	Forest	Compartment	Source ¹	UTM zone	UTM E (m)	UTM N (m)	Objective	Plots ²	Established	Birth ³
CN	Nødebo	Grib Skov	39	Map	32	708585	6211669	Production	1	1898	1843
CO	Tisvilde-Frederiksværk	Hegn						Production	1	1900	1869
DØ	Oreby	Berritzgård Skov	158	Map	32	672680	6082800	Production	2	1956	1907
DÆ	Hørsholm	Rude Skov	469	Map	32	718376	6194196	Production	21	1950	1927
DA	Brahetrolleborg	Bremerhave	211/1900	Map	32	588609	6108514	Production	1	1902	1843
DB	Brahetrolleborg	Bremerhave	211/1900	Map	32	588609	6108514	Production	1	1902	1843
DC	Buderupholm	Sønderskov	159a	Map	32	551794	6296063	Production	1	1906	1847
DD	Buderupholm	Sønderskov	151a:e	Map	32	552291	6296811	Production	1	1906	1847
DE + DEX	Odsherred	Kongsøre	246b	Map	32	670310	6190174	Production	2	1852	1793
DF	Sandbjerg	Storskov	8	Map s. 38	32	547981	6091001	Production	1	1921	1870
DI	Sønderborg	Skjelle Koppel	331/1927	Map	32	548857	6078584	Production	1	1890	1798
DL	Halsted Kloster	Katager	145					Production	1	1923	1881
DM	Halsted Kloster	Torrig	218	Map	32	648432	6087941	Production	1	1923	1881
DN	Boller	Grund Skov	5, 6, 7, 8, 9,16, 17/1924					Production	11	1931	1821
DO	Boller	Grund Skov	333-338/1933	Map	32	555484	6171842	Production	19	1931	1821
DP	Bregentved	Tottrup skov	8	Map	32	699847	6135291	Thinning	11	1938	1919
DQ	Bregentved	Nyskov	560a	Map	32	695747	6136389	Thinning	11	1941	1916
DR	Ravnholt	Dyrehaven	8	Map	32	598504	6124466	Production	1	1938	1894
DS	Ravnholt	Yderste Tve-lykke	XIII, 2	Map	32	600872	6123400	Production	1	1903	1862
DT	Valdemar Slot	Bregninge Skov	III,13	Map	32	604661	6101265	Thinning	4	1941	1919
DU	Valdemar Slot	Bregninge Skov	III,12	Map	32	604802	6101470	Thinning	6	1941	1917

¹Numbers refer to the Establishment Report at *Forest & Landscape*, ²Total number of plots in the experiment of which all may not be beech, ³Seed year

Table B.1: Overview of the individual experiments used in the analyses.

Experiment	District	Forest	Compartment	Source ¹	UTM zone	UTM E (m)	UTM N (m)	Objective	Plots ²	Established	Birth ³
DV	Krenkerup	Fruemose	79	Map	32	676443	6076703	Production	2	1938	1870
DX	Petersgård	Stensby	III 33: 39	Map	32	695602	6095794	Provenance	8	1945	1925-26
DZ	Petersgård	Viemose	34	Map	32	701854	6101048	Provenance	7	1947	1925-29
EB	Gråsten	Sønderskov	216	131	32	553299	6084368	Thinning	6	1962 1964	1941
EC	Gråsten	Blommeskøbel	154	132	32	564981	6090294	Thinning	5	1962	1942
EE	Bregentved	Ganneskov	850d:P:f:g	Map	32	701189	6132659	Species	4	1957	1965
K	Odsherred	Grønnehave	45	Map	32	666493	6199889	Production	1	1872	1953
KAL 1	Fussingø	Hestehave	950a	Map	32	591067	6239417	Regeneration	3	1995	1962-65
KAL 2	Fussingø	Hestehave	950a:952a:b	Map	32	591242	6239536	Regeneration	3	1995	1955
KAL 3	Fussingø	Hestehave	952b	Map	32	591144	6239466	Regeneration	3	1995	1848
LÆ	Bregentved	Boholte	310a	395	32	692032	6139993	Thinning	4	1980	1902
M	Odsherred	Stokkebjerget	191	Map	32	669741	6192745	Production	1	1872	1882:
Q	Jægersborg	Jægersborg Hegn	58q	Map	32	722410	6190868	Production	1	1886	1902:
R	Jægersborg	Geelskov	638b	Map	32	718447	6189899	Production	1	1887	1921
S	København	Geel Skov	345a	Map	32	667473	6151216	Production	1	1887	1946
SOG1	SorøAkademi	Lille Bøgeskov	345a	Map	32	667473	6151216	Regeneration	3	1996	1963
SOG2	SorøAkademi	Lille Bøgeskov	345a	Map	32	667473	6151216	Regeneration	3	1996	1957
SOU1	SorøAkademi	Lille Bøgeskov	334a	Map	32	666791	6152070	Regeneration	3	1996	1819
											1870

¹Numbers refer to the Establishment Report at *Forest & Landscape*, ²Total number of plots in the experiment of which all may not be beech, ³Seed year

Table B.1: Overview of the individual experiments used in the analyses.

Experiment	District	Forest	Compartment	Source ¹	UTM zone	UTM E (m)	UTM N (m)	Objective	Plots ²	Established	Birth ³
SOU2	SorøAkademi	Lille Bøgeskov	334a	Map	32	666791	6152070	Regeneration	3	1996	1939
U	København	Rude Skov						Production	1	1887	1793
X	Odsherred	Stokkebjerg		Map	32	669691	6192849	Production	1	1852	1815

¹Numbers refer to the Establishment Report at *Forest & Landscape*, ²Total number of plots in the experiment of which all may not be beech, ³Seed year